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RESPONSE OF ARCTIC SEDGES TO SIMULATED GRAZING BY MUSKOXEN

BY

YVES PINSONNEAULT

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A thesis submitted to the faculty of Graduate Studies and Research
in partial fulfilment of the requirements for the degree of Master of Science.

DEPARTMENT OF ZOOLOGY

Edmonton, Alberta

FALL 1995

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The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled RESPONSE OF ARCTIC SEDGES TO SIMULATED GRAZING BY MUSKOXEN submitted by YVES PINSONNEAULT in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

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DATE: 19 April 1995

ABSTRACT

The muskoxen (*Ovibos moschatus*) population on Victoria Island has been increasing since the 1970s. This population increase has raised concerns about the impact muskoxen may have on graminoids (sedges and grasses). A clipping experiment (20 m x 20 m; n = 3) was performed in sedge meadows to investigate the effects of simulated grazing (clipping) by muskoxen on above-ground productivity, silica (physical defense) and nitrogen (index of nutritive quality) concentrations in arctic sedges. Objectives of my study were threefold. Firstly, I determined the seasonal pattern of above-ground biomass, silica and nitrogen concentrations in sedges during the summer. Both the above-ground biomass and silica concentration in sedges increased during the growing season. Depending on which meadow was sampled, sedges at least tripled their above-ground biomass throughout the summer, while silica concentrations almost doubled during the same sampling period. In contrast, nitrogen concentrations were primarily high in the early season and decreased over time. Secondly, I determined how the above-ground productivity of sedges was affected when clipped once (4 x 10-day intervals), and at different frequencies (two, three, or four times) during the summer. Daily above-ground productivity of sedges was not significantly different than controls when clipped either at different times or frequencies. Therefore, I concluded that sedges did not compensate for their loss of leaf material. Finally, I determined whether changes in silica and nitrogen concentrations in sedges were produced by both types of clipping. Timing and frequency of clipping had no effect on silica concentration in sedges. Similarly, nitrogen concentrations in sedges were not affected by both clipping treatments, although at one site the concentrations increased, possibly a result of a natural flooding that occurred during the growing season. This study is unique because it investigated effects of simulated grazing on silica (a possible defense against grazing), in conjunction with productivity and nitrogen (index of nutritive quality) in arctic sedges. This integrative experiment contributes to the understanding of sedge-muskoxen interactions, which in turn could improve our knowledge of changes in populations of muskoxen.

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I. GENERAL INTRODUCTION

Since the turn of the century, populations of muskoxen (*Ovibos moschatus*) have remained low in the Canadian Arctic (Tener 1965) through the pressures of hunting and severe winters (Gunn 1990). Subsequent to the 1970s, the population of muskoxen increased (Gunn 1984), particularly on Victoria Island, where the total number of muskoxen has almost tripled from 1983 to 1988-1990 (11 020 to 30 650; see Ferguson and Gauthier 1992). Factors such as year-to-year variation in weather (Caughley and Gunn 1993), and alterations in plant communities (Macnab 1985) are suggested to be responsible for changes in populations of vertebrate herbivores.

The increasing Victoria Island muskoxen population makes it important to study the effects of grazing on northern plant communities and to increase understanding of plant-herbivore interactions. With regard to the muskoxen population increase, Gunn (1991) stated that "[o]ur ability to respond to questions raised by those rapid changes is, however, comprised by our ignorance of the dynamics of the relationship between arctic ungulates and their forage which in turn inhibits our understanding of the population dynamics". Hence, vegetation studies are important to predict what occurs at the population level.

During the summer muskoxen graze predominantly in wet meadows (Parker and Ross 1976; Wilkinson *et al.* 1976; Parker 1978; Thomas and Edmonds 1984; Klein and Bay 1990) to maximize their rate of forage intake (Gunn 1991; Klein 1992). Wet meadows are important grazing areas for muskoxen because plants such as sedges and grasses (*i.e.*, graminoids) grow rapidly and are of high nutritive quality (Klein 1970). Consequently, graminoids dominate the diet of muskoxen during the summer (Tener 1965; Thing 1984; Klein and Bay 1990; Klein and Bay 1991).

Grazing by muskoxen is an important factor that determines the productivity and structure of plant communities (Jefferies 1988; Jefferies *et al.* 1992) by altering

the primary productivity, decomposition, and redistribution of nutrients (Batzli 1978). Such changes in the ecosystem are directly related to the response of individual plants. Specifically, grazing by muskoxen affects plant characteristics such as death rate and growth rate (Crawley 1983).

In general, death rates of plants are only slightly influenced by herbivory, while in contrast, growth rates of plants are directly affected if grazing removes photosynthetic tissues, alters carbohydrate balance, and restricts uptake of water and nutrients (Crawley 1983). Consequently, plants respond to such changes in three different ways (Dyer 1975; McNaughton 1979a; Dyer *et al.* 1982): 1) plant growth is either negatively affected when the intensity of grazing increases (undercompensation); 2) maintained at certain intensities of grazing (equal compensation) and then decreases when grazing intensities increase; 3) or surpasses that of controls at low to moderate intensities of grazing (overcompensation; Belsky 1986). The overcompensation response is described as the herbivore-optimization model (McNaughton 1979a). Compensatory growth may be achieved if photosynthetic capacity is increased, nutrients are reallocated and recycled (faeces and urine), leaf shading is reduced, light efficiency increased, and senescence is reduced (McNaughton 1979b). Other responses of plants to grazing may include changes in secondary metabolites (*e.g.*, tannins and alkaloids), physical defenses (*e.g.*, silica), and nutrients (*e.g.*, nitrogen and phosphorus; Lindroth 1989).

In graminoids the investment of secondary metabolites is minimal because these plants allocate their resources for rapid growth. This allocation strategy supports the resource availability hypothesis described by Coley *et al.* (1985). If graminoids invest little in secondary metabolites, the question then arises: Is there another mechanism by which graminoids can protect themselves against vertebrate herbivores? Silicification has been proposed as a defense against grazing by McNaughton and Tarrants (1983), and McNaughton *et al.* (1985); they reported the concentration of silica in african grasses increased in response to simulated grazing (*i.e.*, clipping), and

therefore concluded that silica could be considered a defense mechanism against vertebrate grazing. In contrast, experiments done on temperate north american grasses found that the concentration of silica either decreased or did not respond to grazing (Brizuela *et al.* 1986; Cid *et al.* 1989; Cid *et al.* 1990).

The contradictory results found in african and north american studies raise the question: "How does the concentration of silica in arctic plants change in response to grazing?". An increase in silica concentration may have important consequences for plant-herbivore interactions occurring in the Arctic. Muskoxen may experience possible effects such as increased tooth wear, reduced digestibility and palatability of plants, and reduced forage intake. These effects may consequently determine the grazing behaviour of muskoxen; however, few conclusions can be made on the basis of silica concentrations alone. For this reason, studying the effects of grazing on both the productivity and nutrient quality (*e.g.*, nitrogen) of arctic plants, with silica, would improve our understanding of the possible responses of arctic plants to herbivory.

The general objective of my study is to determine how productivity, silica and nitrogen concentrations in arctic sedges respond to simulated grazing (*i.e.*, clipping). I organized the thesis into two sections following this general introduction (Section I). In Section II, I review the response of these three plant characteristics to natural and artificial defoliation, with a specific focus on arctic graminoids. In Section III, I present the results of a field experiment I conducted on Victoria Island, Northwest Territories, where I attempted to determine changes in productivity, silica and nitrogen concentrations in arctic sedges subjected to simulated grazing by muskoxen.

II. EFFECTS OF DEFOLIATION ON GRAMINOIDS: A REVIEW

2.1. Introduction

Herbivores can alter the productivity, physical defenses (*i.e.*, silica), and chemical compostion (*i.e.*, nutrients) of plants (Lindroth 1989). The response of individual plants to defoliation can be assessed by two methods: clipping (artificial) and grazing (natural). Limitations between these two types of defoliation should be recognized and considered when interpreting results (Culley *et al.* 1933; White 1973).

An important advantage of clipping over grazing is that clipping allows control of the timing and frequency of defoliation, and the amount of plant biomass removed (Archer and Tieszen 1980). Also, clipping may be less detrimental than grazing because no ungrazed plants are able to gain an advantage or compete for water and nutrients (White 1973). On the other hand, clipping removes biomass uniformly at pre-determined heights, and does not necessarily simulate a herbivore's preference for specific plant species (Culley *et al.* 1933) or parts of the plant (Jameson 1963). As well, in clipped quadrats there is no trampling by herbivores (Culley *et al.* 1933), and a greater amount of biomass is removed suggesting a more severe effect than grazing (Jameson 1963). Furthermore, clipping may be more detrimental than grazing when clipping removes herbage from all tillers (structural units) of a graminoid plant, thus preventing the transfer of carbohydrates between tillers (White 1973; Mattheis *et al.* 1976). Despite these limitations, clipping is a valuable method to determine the response of plants to different timing and frequencies of defoliation (Culley *et al.* 1933).

The objective of this review is to present the effects of defoliation on the net production, silica and nutrient concentrations in arctic graminoids. This review will also serve to introduce my field experiment on the effects of clipping on arctic wet meadow species.

2.2. EFFECTS OF DEFOLIATION ON NET PRODUCTION

Herbivory has long been seen to have a negative impact on the productivity and fitness of plants because photosynthetic surfaces and nutrient supplies are reduced when leaves and stems are removed (Belsky 1987). Several authors have opposed this view and presented evidence that herbivory may be, or is, beneficial to plants by increasing their productivity (equal or overcompensation; ; Dyer 1975, McNaughton 1979a,b; Dyer *et al.* 1982; McNaughton 1983; McNaughton *et al.* 1983; Wallace *et al.* 1983; Belsky 1986; Paige and Whitman 1987; Maschinski and Whitham 1989; Paige 1992) and fitness, which suggests a mutualistic relationship between grasses and grazers (Owen and Wiegert 1976; Owen 1980; Owen and Wiegert 1981).

Belsky (1986) reviewed the literature on the beneficial effects of herbivory and argued that the evidence supporting an increase in productivity and fitness in response to grazing was lacking, and misinterpreted (Belsky 1987; Belsky *et al.* 1993; Painter and Belsky 1993). A previous review by Ellison (1960) reported the same lack of evidence to support the benefits of herbivory to plants. In order for an increase in productivity and fitness to occur, plants would have to be moderately grazed and grown in monocultures where soils were wet and rich in nutrients (Belsky 1987; Painter and Belsky 1993).

McNaughton (1986) is one of the strongest proponents of compensatory plant growth (*i.e.*, equal or overcompensation; Belsky 1986), and is consequently opposed to Belsky's (1986) view that evidence for this type of plant response is lacking. McNaughton (1993) also argued that the debate does not contribute to scientific advancement, and that hypothesis testing should be promoted to refute the beneficial effects of herbivory.

The debate has focused primarily on north american and african studies but has, perhaps unintentionally, not addressed the effects on productivity of graminoids

by artificial or natural defoliation in the sub-arctic or arctic, except for a study by Cargill and Jefferies (1984). The objective of the following review section will be to present the results of sub-arctic and arctic studies, and consequently determine how the productivity of graminoids responded (*i.e.*, under, equal or overcompensation; Belsky 1986) to artificial or natural defoliation.

2.2.1. Response of Arctic Graminoids to Defoliation

Responses of arctic plants to artificial or natural defoliation have not been investigated regularly (Archer and Tieszen 1983). Experiments that have addressed the response of graminoid productivity can be divided into three categories: studies have either determined the general response of graminoids to defoliation, or focused on the impact of artificial or natural defoliation by lesser snow geese in salt marshes of the sub-arctic region (Bazely and Jefferies 1989; Cargill and Jefferies 1984; Zellmer *et al.* 1993), or by rodents (*i.e.*, lemmings; Mattheis *et al.* 1976) and ungulates (*i.e.*, caribou, muskoxen (Henry and Svoboda 1994; Ouellet 1992; Raillard 1992) in arctic meadows.

2.2.1.1. General Response to Graminoid Defoliation

The efficiency with which graminoids replace their leaves after defoliation is controlled by timing, intensity and frequency of defoliation as well as the type of leaf producing unit (*e.g.*, shoots for graminoids), and whether or not the apical meristem (where new leaves are produced) is damaged (Archer and Tieszen 1980).

Archer and Tieszen (1980) showed that production of *Eriophorum vaginatum* leaves was stimulated when clipped once at moss level during the growing season. Reduction of shading (Woledge 1978) or the delayed senescence of older leaves (Archer and Tieszen 1980) may also have contributed to this response. Leaf production decreased when *E. vaginatum* was clipped repeatedly (4 times, once every

10 days) during two growing seasons. Response of leaf growth during the first season was similar to when *E. vaginatum* was clipped only once. However, in the following growing season, leaf length and weight decreased by 25% and 50%, respectively, compared to controls. Stem base and sheath demonstrated similar responses.

This same study also showed that *E. vaginatum* was able to restore photosynthetic tissue only 3 days after defoliation when the apical meristem was intact. In contrast, *E. vaginatum* may cease to produce leaves or may even die when the apical meristem has been damaged or removed (Archer and Tieszen 1980). Contrary to shrubs, *E. vaginatum* exploits the early part of the growing season to increase its photosynthetic tissue (Archer and Tieszen 1980). The authors concluded that early-season defoliation appeared to be less detrimental to *E. vaginatum* than late-season defoliation. Plants clipped in late-season were prevented from recovering because defoliation occurred at a time when light intensity and air temperatures were reduced, thus causing a decrease in photosynthesis. Johnson and Tieszen (1976) found that the photosynthetic capacity of different tundra plants is inversely related to leaf longevity. In that study, deciduous shrubs (*Salix pulchra* and *Betula nana*), sedges (*Carex aquatilis* and *Eriophorum vaginatum*), and evergreen shrubs (*Ledum palustre* and *Vaccinium vitis-idaea*) had the highest, intermediate, and lowest photosynthetic capacities, respectively.

Archer and Tieszen (1983) determined the extent to which different clipping regimes could affect *E. vaginatum*. Over a two year period, sedge tillers were either clipped repeatedly during the first growing season and left to either recover or be clipped the following year. During the first growing season, leaf production appeared to be dictated more by the timing of the initial clipping than by the number of clippings. Tillers clipped early in the season caused a decrease in the cumulative leaf biomass but an increase in leaf length. When clipped during the second growing season, both the cumulative weight and length of leaves were reduced. Leaf biomass of tillers allowed to recover during the second growing season was also significantly

lower than controls (*i.e.,* undercompensated; Belsky 1986) regardless of when clipping was initiated. Leaf length of tillers was comparable to controls when clipping was initiated in early spring, decreased when clipping occurred between late spring and summer, and increased when clipping was initiated in the fall. These results suggest that leaf length is most affected when clipping occurs during the mid growing season. Archer and Tieszen (1983) suggested that leaves of arctic graminoids were capable of tolerating frequent clippings at different times during either one or two growing seasons. Contrary to leaves, biomass of tillers (leaves, stem and sheaths) of *E. vaginatum* suffered more from the number of clippings than from the timing of clippings (Archer and Tieszen 1983).

In all these studies (Johnson and Tieszen 1976; Archer and Tieszen 1980, 1983), the authors did not perform their experiments in more than one site. Although none committed pseudoreplication (experimental units were replicated; Hurlbert 1984), their interpretation of the results would have been more representative of how graminoids respond to defoliation if the experiments had been replicated in several sites. Apart from this limitation, the experimental protocols support reliable conclusions.

2.2.1.2. Graminoid Response to Grazing by Lesser Snow Geese

During the past decade the effects of artificial and natural grazing on graminoids in northern regions (*i.e.,* sub-Arctic and Arctic) has been studied predominantly for lesser snow geese (Cargill and Jefferies 1984; Kotanen and Jefferies 1987; Bazely and Jefferies 1989; Kotanen and Jefferies1989a,b; Hik and Jefferies 1990; Hik *et al.* 1991; Zellmer *et al.* 1993), and for other major herbivores (Mattheis *et al.* 1976) such as rodents and ungulates (Mattheis *et al.* 1976; Ouellet 1992; Henry and Svoboda 1994; Ouellet *et al.* 1994).

In a two-year study, Cargill and Jefferies (1984) examined the effects of natural

grazing by lesser snow geese on the net above-ground primary productivity (NAPP) of *Carex* and *Puccinellia* dominated marshes. During the first year, NAPP of grazed mixed *Carex-Puccinellia* marshes was 35% higher than for ungrazed meadows. During the second year, however, the NAPP of both grazed *Carex* and *Puccinellia* marshes was 77% higher than of ungrazed marshes. This study presents a case for the beneficial effects of grazing because overcompensation (Belsky 1986) of the NAPP was achieved. The study promoted the beneficial effects of herbivory well (Belsky 1987) because temporary exclosures were used, experimental units and sites were replicated, and nitrogen concentrations and below-ground production were measured.

Hik and Jefferies (1990) studied the response of the above-ground biomass and NAPP of grasses to grazing by captive lesser snow geese goslings. Both the above-ground biomass and NAPP of *Puccinellia* dominated marshes increased when grazed at low to moderate intensity (15, 30, 60 and 90 min), and early in the growing season (23 June to 13 July). No response was observed when grazing intensity increased and when grazing occurred later in the growing season. The authors concluded that the presence of goose faeces contributed to the increase of the above-ground biomass and NAPP because grazing alone could not promote such a response.

Additionally, Hik *et al.* (1991) performed a laboratory and field experiment to determine the effects of grazing. The laboratory experiment revealed that the NAPP did not increase when the leaves of *Puccinellia phryganodes* were clipped, however fertilization could improve this response. In the field experiment, the number, timing and frequnecy of grazing events influenced the NAPP of *Puccinellia phryganodes*. The NAPP was significantly higher when plots were grazed three times at regular intervals (12 and 24 days) than when plots were ungrazed, grazed once, or grazed repeatedly during the growing season. Hik *et al.* (1990) suggested that the departure of geese by early to mid-August, 6 weeks prior to winter, allows the plants to recover from the effects of clipping. During this period, plants can restore their carbohydrate and nutrient reserves essential to overwinter survival and growth the following

summer. A similar field study with captive goslings focused on the response of preferred (*Carex subspathacea*) and alternative forage species (*Festuca rubra* and *Calamagrostis deschampsioides*) to grazing (Zellmer *et al.* 1993). No rapid growth response was found.

Differences between grazing and clipping were observed in the studies conducted on *Puccinellia.* The NAPP increased when *Puccinellia* swards were grazed (Cargill and Jefferies 1984; Hik and Jefferies 1990; Hik *et al.* 1991), but decreased when *Puccinellia* was clipped in a laboratory (Hik *et al.* 1991). Because Hik *et al.* (1991) did not discuss the difference between grazing and clipping, I suggest that the different response of *Puccinellia* to the two types of defoliation may be due to factors such as environmental conditions (*e.g.*, light and temperature) and nutrient cycling via goose droppings.

Other studies done to determine the mechanisms involved in the observed increase of NAPP in grazed swards (Cargill and Jefferies 1984) have followed. Changes in leaf and shoot demography are predicted to be responsible for the increase of NAPP in grazed swards. These morphological changes have been studied on dominant graminoids of salt marches: *Carex subspathacea* (Kotanen and Jefferies 1987), and *Puccinellia phryganodes* (Bazely and Jefferies 1989). The number of new shoots in grazed swards of *C. subspathacea* did not differ significantly from ungrazed swards. *C. subspathacea* produced significantly more leaves per shoot in grazed than in ungrazed plots, which would explain the increase in NAPP observed in grazed plots (Kotanen and Jefferies 1987). In contrast, *P. phryganodes* produced significantly more axillary shoots in grazed than in ungrazed swards, but not a significantly greater number of leaves per shoot. A common result in both species was that the life expectancy of grazed leaves was found to be the shortest, thus indicating a rapid turnover of leaves in salt marshes (Bazely and Jefferies 1989). Overall, the results suggest that the increase of the NAPP in grazed swards was achieved in *C. subspathacea* by the growth of existing shoots, while in *P. phryganodes* the increase

of NAPP was achieved by the production of new shoots (Bazely and Jefferies 1989).

Leaf demography has also been investigated for *Carex flavicans* (Kotanen and Jefferies 1989a). Grazing caused a short-term decrease in production and turnover of leaves, but an increase in leaf lifespan (Kotanen and Jefferies 1989a). A different study on the effects of grazing on leaf elongation in *C. flavicans* and *C. subspathacea* did not reveal any significant effect in either species (Kotanen and Jefferies 1989b). The results of this study indicate that leaf elongation does not contribute to explain the observed increase in NAPP in grazed marshes.

2.2.1.3. Graminoids Response to Grazing by Rodents and Ungulates

A study done in Alaska to determine the effects of simulated grazing by lemmings on the leaf production of the sedge *Dupontia fisheri* in wet meadows (Mattheis *et al.* 1976) demonstrated that leaf production was not noticeably reduced when tillers were clipped once either in early or mid-season. However, leaf production decreased slightly when clipped a second time. In addition, when sedges were clipped 6 times during the growing season (*i.e.*, chronically defoliated), productivity was comparable to sedges clipped less frequently (Mattheis *et al.* 1976), hence graminoids appear tolerant of clipping frequency. Tolerance was made possible because defoliated tillers of *D. fisheri* were connected through rhizomes to undefoliated tillers allowing nutrients to flow between them, high concentrations of total nonstructural carbohydrates that buffered the negative effect of grazing were present, and the apical meristem was well protected (Mattheis *et al.* 1976). This response is closely tied with the most favourable of environmental conditions such as an increase in temperature and light, and a more open canopy that occur in early to mid-summer.

The effects of the timing and frequency of simulated grazing by caribou were investigated for the NAPP of two types of sedges: *Carex scirpoidea* from mesic

habitats and *Carex aquatilis*, *Eriophorum angustifolium*, and *Carex membranacea* from wet-meadows (Ouellet 1992; Ouellet *et al.* 1994). The authors showed that when *C. scirpoidea* was clipped once at different times (30 June, 15 July, and 30 July) and repeatedly (3 times) during the growing season, the NAPP was not significantly different from untreated sedges (*i.e*, clipping had no effect). Furthermore, sedges from wet-meadows, when clipped once at different times during the growing season, also compensated. However, repeated clipping significantly decreased (undercompensated; see Belsky 1986) the NAPP. The following year, NAPP was restored for both types of sedges. Sedges appear to have a greater ability to recover from clipping because they begin growth earlier than evergreen and deciduous shrubs (Ouellet *et al.* 1994).

Although the protocol (Ouellet 1992; Ouellet *et al.* 1994) is experimentally sound and presents some interesting results, I question whether or not the response of sedges to clipping is representative across a range of mesic habitats and wet-meadows; afterall, habitat types were not replicated. Time and logistical constraints may have been reasons for not sampling in several habitat types, however no justification for this was given. I addressed site replication in the defoliation experiments presented in Section III.

Henry and Svoboda (1994) compared the above-ground biomass of graminoids from grazed meadows by muskoxen to ungrazed meadows in the high Arctic. The biomass of graminoids available to muskoxen was insignificantly greater in grazed than in ungrazed meadows. From that result, high Arctic graminoids have been described as plants that can tolerate, and perhaps benefit from, moderate grazing despite the short growing season. As well, Raillard (1992) investigated the effects of simulated grazing by muskoxen on the net productivity above 1.5 cm of vegetation in wet meadows in the high Arctic and found no significant differences between the various clipping regimes during four consecutive growing seasons. In short, vegetation in wet meadows (primarily *C. aquatilis* and *E. angustifolium*) compensated for lost tissues.

2.2.2. *Other Factors Determining Growth of Graminoids*

The review section focused primarily on the effects of simulated and natural grazing on the productivity of arctic graminoids. Other than grazing, there are other factors such as temperature, light and nutrients that affect productivity (Tieszen and Archer 1979). An extensive study by Chapin and Shaver (1985) examined these factors on different plant species (*e.g.*, evergreen and deciduous shrubs, and graminoids) where nutrients were predicted to be the most limiting factor of plant growth. Specifically, growth of graminoids (*Eriophorum vaginatum* and *Carex bigelowii*) from tussock tundra was influenced by all three of these factors, while growth of graminoids from wet meadows (*Eriophorum angustifolium* and *Carex aquatilis*) was influenced more strongly by the addition of nutrients. Overall, the study revealed that contrary to what was previously predicted, no single factor limits growth more than the others. In other words, growth of each plant species was limited by a combination of factors (Chapin and Shaver 1985).

2.2.3. *Conclusion*

The literature reviewed on the effects of artificial (clipping) or natural (grazing) defoliation on arctic or sub-arctic graminoids showed compensatory growth to occur in most studies; graminoids appear to be tolerant (Jung *et al.* 1979) when moderately clipped or grazed early in the growing season. However, silica deposition has been proposed as a mechanism for graminoids to protect themselves against defoliation (McNaughton *et al.* 1985). The following section will review the literature dealing with this proposed defense strategy.

2.3. EFFECTS OF DEFOLIATION ON SILICA CONCENTRATIONS IN GRAMINOIDS

The transport of silica from soil to plants has been extensively studied (Jones and Handreck 1967; Lewin and Reimann 1969; Cheng 1982; Raven 1983; Sangster and Hodson 1986). Uptake of silica by plants (Jones and Handreck 1969), deposition (Sangster 1970) and distribution among plant parts (Kaufman *et al.* 1981) are some of the most researched aspects of the silica cycle. Studies of silica have focused primarily on economically important plants such as rice (Yoshida *et al.* 1959; Yoshida *et al.* 1962), oats (Jones and Milne 1963; Handreck and Jones 1968), sugar cane (Fox *et al.* 1969) and wheat (Hutton and Norrish 1974; Jarvis 1987; Mayland *et al.* 1991). However, interest in the biological significance of silica has led researchers to also examine the management implications of silica on non-commercial plants and the herbivores that consume them. Such studies have examined whether or not silica increases as a result of simulated grazing, as well as the possible effects (*e.g.*, food preference and diseases) silica may have on herbivores. The objectives of this section are to (1) give some background information about the transport of silica from soil to plants, (2) present results of the few experiments that have examined the response of silica to artificial defoliation, (3) report the effects silica may have on the food preference of herbivores, and (4) consequences for herbivores ingesting silica.

2.3.1. Silica in Graminoids

Silica enters a plant as water soluble monosilicic acid $Si(OH)_4$, and is transported to roots, stem, and leaves (Barber and Shone 1966; Sangster and Parry 1981). Typically, the amount of silica in a plant is directly associated with the amount of water absorbed (Lanning *et al.* 1958), and as water is lost, polymerization takes place to form amorphous silica ($SiO_2 . nH_2O$) (Kaufman *et al.* 1981). Silica is deposited in the cell lumen (Sangster and Parry 1981), cell wall (Jones *et al.* 1963), and intracellular spaces of a plant (Parry and Smithson 1964). Once deposited and

solidified, silica becomes immobile and cannot be retranslocated (Handreck and Jones 1968), thus becoming unavailable to other parts of the plant (Yoshida *et al.* 1962).

The concentration of silica in grasses varies with species, soil type and transpiration rate (Van Soest 1982). For example, monocotyledons (*e.g.*, sedges) accumulate 10 to 20 times more silica than dicotyledons (*e.g.*, legumes; Jones and Handreck 1967). Silica concentration in plants can to be as high as 3% to 5% dry matter weight (Smith *et al.* 1971). Bezeau *et al.* (1966) described the silica concentration in grasses and sedges to vary from 0.87 % to 5.44%, and averaging 2.61% in fescue grassland. However, Staaland and Olesen (1992) found only 1.1% silica in arctic graminoids from west Greenland in the summer.

Silica may serve structural, physiological and protective functions in plants (Jones and Handreck 1967). Structurally, silica complements lignin as it strengthens and rigidifies the cell wall (Van Soest 1982), helping leaves become more erect as concentration increases (Jones and Handreck 1967). Physiologically, silica increases the photosynthetic surface and efficiency of leaves (Cheng 1982; Adatia and Besford 1986), and improves the supply of oxygen to roots (Jones and Handreck 1967). Resistance to pathogens, insects and grazing by herbivores are some of the protective functions of silica in plants. Silica decreases the digestibility (Van Soest and Jones 1968) and palatability of plants (Jones and Handreck 1967), increases tooth wear in herbivores (Baker *et al.* 1959), and causes a condition in vertebrate herbivores known as silica urolithiasis (silica particles deposited in the urinary tract to form obstructive calculi; Bailey 1981).

2.3.2. Response of Silica to Artificial Defoliation

Few researchers have attempted to determine whether or not silica increases as a response to artificial defoliation. Experiments addressing this question can be classified into two geographic groups: those done on african grasses, and those on

north american grasses.

Studies on african grasses have shown that silica concentration increase following artificial defoliation (McNaughton and Tarrants 1983; McNaughton *et al.* 1985). In a laboratory experiment, McNaughton and Tarrants (1983) studied the effects of defoliation, origin (*i.e.*, heavily *versus* lightly grazed), and species on the leaf silicification of three african grasses. The addition of soluble silicates in the nutrient medium was also studied. Results showed that silica concentration in artificially defoliated grasses (3.48%) was 1.8 times greater than controls (1.97%), and grasses that originated from a heavily grazed area (3.86%) had a greater (1.7 times) silica concentration than those from a lightly grazed area (2.31%). Finally, silica concentration in *Eustachys paspaloides* (3.32%) was 1.7 times greater than the average in *Adropogon greenwayi* and *Panicum coloratum* (1.90%). The addition of soluble silicates in the nutrient medium did not increase the net production of grasses. Significant effects of the different defoliation treatments, areas and species provide insight into the dynamic interaction between plants and herbivores. McNaughton and Tarrants (1983) concluded that silicification in grasses promoted by grazing acts as an effective defense against herbivores.

The work of McNaughton *et al.* (1985) complements that of McNaughton and Tarrants (1983) by also assessing the response of silica to artificial defoliation in both a field and a laboratory experiment. Location and time of sampling determined silica concentration in grasses in the field experiment, which were reported to be the highest ever found in grasses ($\geq$ 12%). As well, the average silica concentration in grasses decreased over the growing season.

In laboratory-grown grasses, the concentration of silica decreased in plant parts with increasing distance from the soil. In other words, silica concentration was highest in the roots and lowest in the leaf blades. Artificial defoliation increased the silica concentration in sheaths of *E. paspaloides*, while that of *A. greenwayi* and *P.*

coloratum was unaffected by the treatment. Contrary to McNaughton and Tarrants (1983), the addition of soluble silica in the nutrient medium increased the net production of undefoliated grasses by 18% (McNaughton *et al.* 1985). Despite this increase in net production, silica was not considered to be an absolute growth requirement because no significant differences were found between the net production of grasses grown with and without silica added to the nutrient medium. Leaf blade, leaf sheath, and crown growth were stimulated whereas stem, root and litter production were unaffected.

The increase of silica concentration from leaves to roots and by artificial defoliation led McNaughton *et al.* (1985) to conclude that african grasses take up silica actively, and not passively, as presented in other studies (Jones and Milne 1963; Jones and Handreck 1967). They also suggested that since silica strengthens grasses, the carbon use for this purpose would be used for other roles, thus favouring a better carbon balance in grasses. McNaughton and Tarrants (1983), and McNaughton *et al.* (1985) proposed that the patterns of silicification (*i.e.*, differences within and between species, and past and present grazing exposure) in african grasses have contributed to a better understanding of the coexistence and radiation of grasses and grazers.

I can conclude from these two studies done on african grasses that silica concentration was (1) increased when grasses were artificially defoliated, (2) highest in heavily grazed sites, (3) highest earlier in the growing season, decreasing thereafter, and (4) different between species. Silica concentration in grasses was also reported to decrease from roots to leaves. As well, only McNaughton *et al.* (1985) found the addition of silica in the nutrient medium to increase grass growth.

Although interesting results and conclusions can be drawn from these two studies on african grasses (McNaughton and Tarrants 1983; McNaughton *et al.* 1985), O'Reagain and Mentis (1989) has criticized the validity of the silica increase in response to defoliation. O'Reagain and Mentis (1989) suggested that the response of

silica may have been caused by an increase in transpiration of cut leaves, and not by defoliation. Authors of the african studies (McNaughton and Tarrants 1983; McNaughton *et al.* 1985) should clarify their experimental methods and reply to this criticism. Until such clarification is presented, the results should be interpreted with caution.

Several studies on native north american grasses have been done to compare to the results found on african grasses (Brizuela *et al.* 1986; Cid *et al.* 1989; Cid *et al.* 1990). However, these studies measured the silicon (Si) concentration, as opposed to silica (SiO_2) concentration in the african studies. The silicon concentration can be converted to silica concentration by multiplying by 2.14 (Brizuela *et al.* 1986). Here the findings of each study are presented as silica concentrations to maintain a consistency with the results from the african studies.

Brizuela *et al.* (1986) performed two field experiments that examined the seasonal changes of silica at different sites, and the response of silica when grasses (*Agropyron smithii* and *Schizachyrium scoparium*) were artificially defoliated. They found that silica concentration generally increased over the growing season. Other studies have also shown this increase over time (Handreck and Jones 1968; Cheng 1982), however, the opposite trend was found in african grasses (McNaughton *et al.* 1985). Also, contrary to the findings of McNaughton *et al.* (1985), Brizuela *et al.* (1986) found that silica concentration in artificially defoliated grasses was lower than undefoliated grasses. As in african grasses (McNaughton and Tarrants 1983; McNaughton *et al.* 1985) they also found that grasses from heavily grazed sites had greater silica concentration than those from lightly grazed sites.

The same two questions proposed by Brizuela *et al.* (1986) were studied by Cid *et al.* (1989) in a laboratory experiment. Seasonal changes of silica in undefoliated grasses (*A. smithii*) confirmed the increase over time found by Brizuela *et al.* (1986). At both the heavily grazed and exclosure sites, defoliated grasses also had

a lower silica concentration than undefoliated grasses. Silica concentration in grasses from the heavily grazed site (4.7%) was significantly greater than those from the exclosure site (4.1%). Additionally, Cid *et al.* (1989) found morphological (*e.g.*, leaf blade length and width) differences between grasses from the heavily grazed and exclosure sites.

Cid *et al.* (1990) continued their previous work by examining how silica responds to defoliation and different grazing history of sites, and how it is distributed within grasses (*A. smithii*). Unlike Brizuela *et al.* (1986) and Cid *et al.* (1989), no significant differences were found in the silica concentration of shoots between defoliation treatments (*i.e.*, defoliation *versus* control) and grazing history (*i.e.*, heavily grazed *versus* exclosure). Defoliated grasses significantly increased their shoot production above clipping height, possibly a consequence of the clipping interval and duration of the experiment, which was longer (*ca.* 20-23 weeks) than other similar studies (Polley and Detling 1988; Painter and Detling 1981). This increase in biomass of defoliated grasses appears to explain the low silica concentration found in grasses. The results of this experiment also demonstrated that defoliated shoots had a lower silica concentration than undefoliated shoots. Vertical distribution of silica in grasses was different between plant parts but similar between the two sites sampled. Roots and leaf blades had the greatest silica concentrations, however within the shoot, silica concentrations decreased with decreasing distance from the roots.

In contrast to the findings on african grasses, silica concentration in shoots of north american grasses (1) in general decreased when artificially defoliated, (2) increased throughout the growing season, and (3) decreased with decreasing distance from the roots. A possible explanation for the different responses in the silica concentration of both groups of studies could be attributed to differences between the species and the origin of grasses. As well, the solubility of silica is reduced in colder environments and by shorter growing seasons (Sangster and Hodson 1986).
Besides the differences reported, one similarity was found between the two groups of

studies; grasses from heavily grazed sites had greater silica concentrations than lightly grazed sites on both continents.

2.3.3. Effects of Silica on Food Choice

Food choice experiments have been done to determine the importance of silica as a defense against herbivores. In a study by Gali-Muhtasib *et al.* (1992) two species of grasses with known but variable concentrations of silica and nitrogen were offered to voles. In a first experimental design, nitrogen was found to dictate the food selection whereas silica was second in importance. No significant differences were found between the two grass species. Food consumption by voles was inhibited by silica only when the nitrogen concentration in both the treatment and standard samples was the same. In another experimental design, pairwise combinations of the two grass species with two silica and nitrogen concentrations (n = 8) were offered to voles. Here silica was found to be the most influential factor; voles preferred grasses grown with less silica, independently of species and nitrogen concentration. Thus, Gali-Muhtasib *et al.* (1992) suggested that small vertebrate herbivores evaluate both the silica and nitrogen concentration in grasses before consuming them.

Previous to this experiment, silica was found to decrease the grazing intensity of snails on rice plants (Wadham and Parry 1981). McNaughton and Tarrants (1983) referred to this study to support that "silicification can act as an effective deterrent to herbivory". By implying that the result found in a single study on invertebrates could be applied to vertebrate herbivores, especially when no controlled study between the silica concentration in plants and the preference of vertebrate herbivores had been performed at that time (Gali-Muhtasib *et al.* 1992), I believe McNaughton and Tarrants (1983) were ambitious in their conclusion.

In contrast, Brizuela *et al.* (1986), Cid *et al.* (1989), and Cid *et al.* (1990) failed to determine that silica is an effective defense against vertebrate herbivores.

Even though silica concentration was found to be greater in a heavily grazed site (4.7%) than in a lightly grazed site (4.1%), bison grazed preferentially in the former (Coppock *et al.* 1983; Krueger 1986). Such a small difference in the silica concentration between the two sites (*i.e.*, heavily and lightly grazed) was insufficient to offset the higher nitrogen concentration promoted by grazing at the heavily grazed site (Coppock *et al.* 1983; Krueger 1986). In addition, Shewmaker *et al.* (1989) reported that the food preference of sheep was not influenced by the silica concentration in grasses.

The opposing results found from these few experiments on the effects of silica on the food preference of herbivores suggest that the work should be pursued following the experimental design of Gali-Muhtasib *et al.* (1992). However, grasses should be grown with a greater combination of different silica and nitrogen concentrations, and not with only two concentrations. The proposed experiment would give more insight into the effects of the interaction between silica and nitrogen in foods consumed by herbivores.

2.3.4. Consequences of Herbivores Ingesting Silica

When herbivores graze they ingest plants with different concentrations of silica, and as a result may experience some detrimental effects such as an increase in tooth wear. Baker *et al.* (1959) demonstrated that silica is harder than tooth enamel, and therefore concluded that silica is an abrasive agent that could accelerate tooth wear in domestic sheep. However, the importance of this result has not been applied beyond a laboratory application, and consequently the biological significance of this effect has not been investigated. Certain questions should be posed to provide a better insight into the importance of silica in accelerating tooth wear of herbivores. Does the increase in tooth wear affect the condition of a herbivore during its lifetime, and if so, how? And, are herbivores affected to such an extent that an increase in tooth wear would regulate population size? These questions should provide the background for

further research in this area.

Other effects of ingesting silica include a decrease in the digestibility of plants. Van Soest and Jones (1968) found that silica accounted for 58% of the variance in digestibility of grasses from humid climates, and concluded that silica was an important factor limiting digestibility in vertebrate herbivores. In contrast, Smith *et al.* (1971) found that silica accounted for only 3% of the variance in digestibility of grasses from dry climates; hence, silica is not as important in limiting the digestibility of grasses as previously studied by Van Soest and Jones (1968). Results of these two studies would lead us to predict that silica would reduce the digestibility of arctic graminoids from wet meadows. Palatability of plants has also been shown to decrease as a result of an increase in silica concentration (Jones and Handreck 1967). Furthermore, once plants are digested, silica may be responsible for a disease known as silica urolithiasis (Bailey 1981).

2.3.5. Conclusion

Response of silica to artificial defoliation was found to differ between subtropical african grasses (increase) and temperate north american grasses (decrease or no effect). However, the effect of artificial defoliation on silica concentration in arctic plants has never been investigated. An experiment that determined the response of silica to simulated grazing by muskoxen in arctic sedges is presented in Section III.

In some cases, silica has been shown to strongly influence the food choice of herbivores. Nutrients in plants (*e.g.*, nitrogen and phosphorus) are also important factors influencing what herbivores consume (Lindroth 1989). Artificial or natural defoliation can change the nutrient concentration in plants, and experiments that have presented such changes are reviewed in the following section.

2.4. EFFECTS OF DEFOLIATION ON NUTRIENT CONCENTRATIONS IN GRAMINOIDS

Food quality is an important factor that can affect different facets of herbivores such as growth, reproduction and mortality (Crawley 1983). Beyond productivity and physical defenses (silica), which were previously reviewed, food quality (*e.g.*, nitrogen and phosphorus) can also be altered by artificial and natural defoliation.

In sub-arctic and arctic regions, tundra plants produce a relatively small amount of biomass with high nutrient content, suggesting an adaptation to nutrient-poor habitat (Chapin *et al.* 1975). However, the short supply of nutrients may limit the productivity of plants since they respond favourably to the addition of nutrients (Chapin *et al.* 1975; Henry *et al.* 1986). Reduced availability of nutrients is responsible for the occurrence of a negative chain reaction (*i.e.*, decrease in nutrient absorption, photosynthesis, and growth; Bryant *et al.* 1983).

Because of the short growing season, rapid leaf production in many arctic graminoids occurs soon after snow-melt with the support of large below-ground reserves of nutrients and carbohydrates (Dennis *et al.* 1978; Bryant *et al.* 1983). Nitrogen and phophorus are nutrients that most commonly limit growth of plants (Chapin *et al.* 1980). Seasonal distribution of nitrogen and phosphorus in plants provides a basis to predict the effects of timing and frequency of defoliation (Chapin *et al.* 1980). During the growing season, nitrogen concentration increases until approximately two weeks after snow-melt (late June to mid-July), and thereafter decrease as the season progresses (Chapin *et al.* 1975; Chapin 1977; Chapin 1980a; Chapin *et al.* 1980; Raillard 1992; Ouellet *et al.* 1994). In contrast, phosphorus concentration generally decreases during the entire growing season (Chapin *et al.* 1975; Ouellet 1992; Ouellet *et al.* 1994). The seasonal decrease of both concentrations is promoted by the addition of secondary cell walls and subsequently by the downward translocation to below-ground biomass (Chapin 1977). The

objective of this review section is to present how the seasonal distribution of nitrogen and phophorus concentrations of arctic graminoids are affected by artificial and natural defoliation.

2.4.1. Response of Nitrogen and Phosphorus to Artificial and Natural Defoliation

I followed a similar approach to the section on productivity to review the effects of artificial and natural defoliation on the nutrient concentration of sub-arctic and arctic graminoids. In other words, the effects of natural defoliation by lesser snow geese in the sub-Arctic, and simulated grazing by ungulates (clipping) in the Arctic will be reviewed.

Chapin (1980a,b) determined that the nitrogen and phosphorus concentrations of *E. vaginatum* doubled from mid-June to late August when clipped repeatedly at 10-d intervals and also when clipping was initiated at different times during the growing season. Nitrogen and phosphorus concentrations of undefoliated leaves also increased over the season, albeit less than defoliated leaves, and decreased during August. Similar changes were observed for *C. aquatilis*.

As a consequence of defoliation, Chapin and Slack (1979) measured the capacity of roots to absorb phosphates by two sedges, *E. vaginatum* and *C. aquatilis*. The authors found that the nitrogen and phophorus reserves in roots (dry weight) were not significantly altered by any treatment. However, when concentrations were measured on the basis of root length, nitrogen was unaffected by the treatments, but phosphorus significantly decreased with increasing defoliation.
The phosphorus absorption rate of *E. vaginatum* was significantly higher than control roots when clipped once. However, when clipped four times, the absorption rate was significantly lower than control roots. In contrast, phosphate absorption rate of *C. aquatilis* was not affected by one or two defoliations, and increased when clipped four times. Thus, the authors concluded that the rate of phosphate absorption of *C.*

aquatilis is less sensitive to defoliation than *E. vaginatum* because of larger below-ground biomass (Chapin and Slack 1979).

Besides clipping, temperature of soils is another factor that can affect the capacity of plants to absorb phosphates (Chapin 1974a,b; Chapin and Bloom 1976; Chapin 1977). As soil temperate increases, the rate of absorption increases for members of the genera *Dupontia*, *Carex*, and *Eriophorum* (Chapin and Bloom 1976). In comparison to warmer climate plants, arctic graminoids, especially wet sedge species, have a greater potential to acquire phosphorus because of large root biomass and a greater affinity of absorption (Chapin 1974b; Chapin and Bloom 1976; Chapin 1977).

2.4.1.1. Nitrogen and Grazing by Lesser Snow Geese

Changes in the productivity of graminoids in response to lesser snow geese grazing were previously reviewed (Cargill and Jefferies 1984; Hik and Jefferies 1990; Hik *et al.* 1991; Zellmer *et al.* 1993). These authors also investigated the changes in the concentration of nitrogen, and results of these studies are reviewed below.

Cargill and Jefferies (1984) determined the total nitrogen concentration of grazed *Carex* and *Puccinellia* marshes by lesser snow geese to be significantly higher than in ungrazed marshes during a two-year study. Generally, trends for both years showed that the nitrogen concentration decreased during the growing season for both species. However, nitrogen concentration in *Carex* was significantly greater than in *Puccinellia* and was, for both species, higher during the first year. During the second year, the cumulative total quantity of nitrogen deposited in shoots in both species was calculated to be greater in grazed sites (3.0-3.5 g m^{-2}) than in ungrazed sites (1.5-2.0 g m^{-2}).

Hik and Jefferies (1990) determined that grazing by captive lesser snow geese goslings increased the nitrogen concentration when above-ground biomass of *Puccinellia* was grazed early in the season at intermediate intensities (15-90 min). Throughout the growing season, nitrogen concentrations decreased, but the rate of decline was less in grazed than in ungrazed shoots. Net accumulation of nitrogen in *Puccinellia* grazed on 23 June and 2 July was almost twice that of ungrazed swards after 36- and 48-d of regrowth. The presence of goose faeces helped promote such in increase in the concentration of nitrogen. When grazed at a later date, the net accumulation of nitrogen was lower at the same time after regrowth.

Hik *et al.* (1991) found that the nitrogen concentration of ungrazed *Puccinellia* decreased during the growing season. When *Puccinellia* was grazed at 12-d intervals, no significant decrease in the nitrogen concentration was observed. At 24-d intervals, the nitrogen concentration of *Puccinellia* was lower than when grazed at 12-d intervals. Statistical analyses revealed that the nitrogen concentration in shoots from plots that were repeatedly grazed (three, four, five and six times) was greater than that of ungrazed shoots. In that experiment, the net accumulation of nitrogen in all grazing treatments was similar until large differences were observed at the end of the season. Plots grazed three, four and five times at 12-d intervals had greater nitrogen quantity than ungrazed plots, and similar results were found when plots were grazed at 24-d intervals.

After studying the effects of grazing on the nitrogen concentration of the main plant species grazed by geese, Zellmer *et al.* (1993) investigated the effects of grazing on alternative plant species: *Carex subspathacea*, *Festuca rubra* and *Calamagrotis deschampsioides*. In this experiment, the nitrogen concentration of shoots following grazing was lower than in ungrazed shoots. Differences between species were observed where *C. subspathacea* (2.4%) had a nitrogen concentration higher than *F. rubra* and *C. deschampsioides* (1.8-1.9%). In all three species, nitrogen concentration declined as the season progressed (Zellmer *et al.* 1993).

2.4.1.2. Nitrogen, Phosphorus, and Simulated Grazing by Ungulates

The effects of simulated grazing by other herbivores such as muskoxen and caribou have also been studied. In the high Arctic, Raillard (1992) simulated grazing by muskoxen (*i.e.*, clipped at 1.5 cm above moss level) to determine the response of the net accumulation of nitrogen in vegetation during four growing seasons (1986-1989). During the experiment, both the seasonal and cumulative (1986-1988) accumulations of nitrogen were determined.

In general, net accumulation of nitrogen in vegetation (all plants from wet-meadow clipped in quadrats) increased with increasing frequency of clipping during each growing season. The greatest nitrogen increase (2*x* greater than plots clipped once) was found during the second season in plots clipped four times. The increase became progressively less pronounced during the following two seasons. The highest cumulative accumulation of nitrogen was found in the vegetation of plots that were clipped either three or four times each season. These nitrogen values were significantly greater than those found in vegetation of plots that were either not clipped or clipped once each season. The highest concentration of nitrogen was found in vegetation clipped four times each season, after three seasons. These results suggest that the uptake of nutrients is maintained during the growing season, and compensation for loss of nutrients occurs (Raillard 1992).

A different approach to defoliation was taken by Ouellet *et al.* (1994) when studying the effects of timing and frequency of simulated grazing by caribou. Contrary to simulated grazing by muskoxen (*i.e.*, 1.5 cm above moss level; Raillard 1992), sedges were clipped at moss level based on direct observations of caribou feeding. Two types of sedges were studied: *C. scirpoidea* from mesic habitats, and dominant species such as *C. membranacea*, *C. aquatilis*, *C. bigelowii*, and *E. angustifolim* from wet-meadows. Sedges from wet-meadows clipped either at different times (15-d interval) or repeatedly (three times) during the growing season increased

their nitrogen and phosphorus concentrations (Ouellet 1992; Ouellet *et al.* 1994). Nitrogen concentration of *C. scirpoidea* showed the same responses to clipping, while that of phosphorus was not assessed.

2.4.2. Conclusion

In most studies, artificial and natural defoliation appeared to favour an increase in nitrogen and phosphorus concentration. In the lesser snow geese experiments, the effect of defoliation (*i.e.*, increase in nutrient concentration) was stronger when plants were defoliated early in the growing season and at moderate intensities. In contrast, clipping experiments that simulated grazing of muskoxen and caribou showed that nitrogen and phosphorus concentrations increased through time and with increased frequency of defoliation. Different trends in the two types of experiments (*i.e.*, artificial and natural defoliation) appear to suggest that the action of either grazing or clipping brings about different results. However, I realize that this conclusion is lessened by the fact that experiments on both types of defoliation were done in different systems. Therefore, to confirm any differences between grazing and clipping, experiments should be performed in the same system.

2.5. Synthesis

This review presented how productivity, silica (physical defense), and nutrients in graminoids responded to artificial and natural grazing. Although few studies have researched the effects of these two types of defoliation in sub-arctic and arctic regions, the experiments reviewed above found that in general, the productivity of graminoids showed compensation (equal or overcompensation), silica concentrations either increased or decreased depending on the origin of the grasses (*i.e.*, Africa or North America), and the concentration of nitrogen and phophorus increased.

Hypothetically, an increase in a herbivore population would entail a greater grazing pressure and, therefore, changes in graminoid communities. An increase in grazing pressure could lead to a series of events: (1) an increase in productivity and quality (nutrients) of graminoids; (2) the subsequent increase in grazing pressure by increasing the numbers of herbivores, and (3) the possible grazing deterrence by increasing concentration of silica through changes in quality (*i.e.*, digestibility and palatability) of graminoids. This increase in concentration of silica could consequently alter where herbivores graze and what plant species they will feed on.

Such a sequence of events are possibly occurring on Victoria Island, Northwest Territories, where the muskoxen population has increased over the past 20 years (Gunn 1984), more particularly from 11 020 in 1983 to 30 650 in 1988-1990 (Ferguson and Gauthier 1992). This rapid population growth may cause potential changes in graminoid communities from an increase in grazing pressure. Never have researchers investigated the simultaneous effects of defoliation on the three characteristics reviewed (productivity, silica and nutrients) for arctic plants. The following section presents an experiment in which the effects of simulated grazing by muskoxen in arctic meadows were studied.

III. RESPONSE OF SEDGES TO ARTIFICIAL DEFOLIATION

3.1. Introduction

Grazing may change the dynamics of vegetation communities by affecting productivity and chemical composition of forage plants (Crawley 1983). With respect to productivity, response of plants to grazing has been described as a continuum from undercompensation to overcompensation in biomass (Belsky 1986; Maschinski and Whitham 1989). Observed effects of grazing on chemical plant defenses have been described by two hypotheses. First, the "apparency" hypothesis (Feeny 1976) suggests that the frequency of plant species dictates whether chemical defenses are qualitative (*i.e.*, toxins) or quantitative (*i.e.*, digestibility-reducing compounds). Common plants generally possess quantitative defenses such as tannins. In contrast, some common plants such as arctic graminoids (sedges and grasses) do not support this hypothesis because they are devoid of tannins (Jung *et al.* 1979). Second, the "resource availability" hypothesis suggests that the increased growth rate of a plant causes the investment in chemical defenses to decrease (Coley *et al.* 1985). Arctic graminoids grow rapidly and possess few chemical defenses, thus supporting this hypothesis. Thus, arctic graminoids are said to be tolerant to grazing (Jung *et al.* 1979).

More recently, researchers have suggested plants use silica to protect themselves against herbivores (McNaughton *et al.* 1985). Herrera (1985) called this hypothesis the "silica defense method" (SDM). Silica decreases the digestibility (Van Soest and Jones 1968) and palatability of plants (Jones and Handreck 1967), increases tooth wear (Baker *et al.* 1959), and can cause silica urolithiasis (*i.e.*, urinary calculi; Bailey 1981).

The concentration of silica in plants responding to artificial defoliation has previously been studied (Brizuela *et al.* 1986; Cid *et al.* 1989; Cid *et al.* 1990; McNaughton and Tarrants 1983; McNaughton *et al.* 1985), but results of those studies

have varied. In one instance, silica concentrations were significantly lower in artificially defoliated grasses than untreated grasses (Brizuela *et al.* 1986; Cid *et al.* 1989; Cid *et al.* 1990). In contrast, McNaughton and Tarrants (1983) and McNaughton *et al.* (1985) found that artificial defoliation significantly increased silica concentration. In the Arctic, the response of silica concentration in sedges to artificial defoliation has yet to be determined.

In contrast to silica, effects of artificial defoliation on the nutritive quality of arctic graminoids have been described (Chapin 1980a,b; Ouellet 1992; Raillard 1992). Below-ground reserves of nutrients and carbohydrates are important to graminoids' response to grazing, since they allow rapid production of new leaves and shoots (Bryant *et al.* 1983). Previous experiments have shown that competition occurs between nutrients such as nitrogen and silica for entry in plants. In other words, when nitrogen concentration of a plant increases, silica concentration is expected to decrease (Wallace *et al.* 1976; Wallace 1989). Although not yet investigated for arctic graminoids, this relationship may be important for herbivores if silica concentration increases as a response to artificial defoliation. The nutritive quality of graminoids may be reduced, which in turn, could alter where herbivores graze and on what plant species they feed.

In the Canadian Arctic Archipelago, numbers of muskoxen have increased since the 1970s (Gunn 1984), and are now estimated at 30 650 on Victoria Island (see Ferguson and Gauthier 1992). Such a continued increase of the population may impact their food sources (Jefferies *et al.* 1992) by altering the productivity, physical defenses (*e.g.*, silica) and chemical composition (*e.g.*, nutrients) of plant communities (Lindroth 1989).

Muskoxen feed heavily in sedge meadows during the summer (Parker and Ross 1976; Wilkinson *et al.* 1976; Thomas and Edmonds 1984; Henry *et al.* 1990), and graminoids dominate their diet at this time (Thing 1984; Klein and Bay 1990; Klein

and Bay 1991). The relationship between muskoxen and graminoids has been referred to by Jefferies *et al.* (1992) as the "pump and idle" model. From June to August, the above-ground productivity of graminoids rapidly increases (*i.e.*, pump) (Savile 1972). Muskoxen take advantage of this rapid growth by increasing their food consumption (Parker and Ross 1976; Klein 1992) to regain fat and protein reserves (White *et al.* 1989). In contrast, muskoxen must reduce their food consumption during winter (January to March) as the productivity of sedges "idles" (Jefferies *et al.* 1992).

This study was designed to assess how sedges respond to simulated grazing by muskoxen. Specifically, I tested whether or not timing and frequency of defoliation promoted changes in above-ground productivity, silica and nitrogen concentrations of arctic sedges. My objectives were to determine: 1) the seasonal pattern of above-ground biomass, silica and nitrogen concentration in sedges during the summer; 2) how defoliation regimes affected the above-ground productivity of sedges (*i.e.*, over, equal or undercompensation); and 3) whether or not simulated grazing promoted silica and nitrogen accumulation in sedges. Both the concentration of silica and nitrogen was determined to establish a comparison between an element that reduces the digestibility of sedges (silica) and one that promotes their nutritional quality (nitrogen).

3.2. Methods and Materials

3.2.1. Study Area

Victoria Island is located immediately north of the canadian mainland and comprises an area of 134 400 km^2. The southeastern region of the Island was described by Polunin (1951) as part of the low-arctic ecosystem, characterized by flat-lying to gently dipping sandstone, minor limestone and dolomite of early Palaeozoic age (Thorsteinsson and Tozer, 1962, Fyles, 1963). The elevation of the lowland areas lies within 150 m above sea-level. The landscape lacks large moraines and is characterized by fields of drumlinoid ridges and feature numerous lakes and rivers for which the drainage is disorganized (Thorsteinsson and Tozer, 1962, Fyles, 1963). Furthermore, the region is characterized by communities of nearly continuous vegetation cover containing over 200 species of vascular plants (Porsild and Coady 1980; Edlund 1983). The area is dominated by species of the genera *Dryas, Potentilla, Rhododendron, Dupontia,* and *Carex* (Bliss *et al.* 1973; Edlund 1983).

From 27 June to 13 August, 1992, I conducted clipping experiments in three sedge meadows that were located 15 km NE of Cambridge Bay, southeastern Victoria Island, Northwest Territories (Fig. 3.1). I used three criteria to select representative sedge meadows: 1) a minimum area of 50 m x 50 m; 2) mesic-hydric moisture regime; and 3) areas dominated by sedges (*e.g., Carex* spp.) and mosses. Characteristics such as the major plant species, relief, slope (increments of 5%), aspect (east, west, north, and south) and area were recorded for each site. Differences between the three sedge meadows were most noticeable in Site 3, which had a higher proportion of mosses, and different biophysical characteristics than Sites 1 and 2 (Appendices 1 & 2).

3.2.2. Seasonal Changes in Above-Ground Biomass, Silica and Nitrogen

Within each of the three sites, I randomly established an experimental plot (20 m x 20 m). I positioned a total of 20 quadrats (1.0 m x 0.5 m) on the perimeter of each experimental plot (5 on each side; Fig. 3.2a). I randomly selected five of those quadrats on each of four sampling dates (27 June, 7 July, 17 July, and 27 July). In each quadrat, I clipped sedges to moss level and air-dried samples in the field.

3.2.3. Defoliation Experiments

I conducted the clipping trials within each of the three experimental plots (Fig. 3.2b). Each plot was divided into 64 sections (8 rows by 8 columns). A quadrat (1.0 m X 0.5 m) was located at the centre of each section and placed parallel to the rows. Two diagonally opposed corners of all quadrats were marked to ensure that the same area was clipped at each visit.

A control and seven treatments for both the timing (*i.e.*, clipped once either on 27 June, 7 July, 17 July or 27 July), and frequency experiments (*i.e.*, clipped two, three, and four times) were studied during the summer (Table 3.1). Treatments were randomly assigned to quadrats (experimental unit) to account for differences among the 64 sections of the clipping plot, and replicated once in each row and column (Sokal and Rohlf 1981). Unexpectedly, Site 3 was naturally flooded between 28 June and 16 July, which prevented any clipping of sedges on 7 July. Consequently, the clipping regime of both experiments was reduced to three events for Site 3, as opposed to four events for Sites 1 and 2.

Arctic sedges typically reproduce vegetatively by producing networks of individual tillers through the development of rhizomes (Shaver and Billings 1975). Since rhizomes can measure 1.0 m in length (Henry 1987), a 1.5 m buffer zone was

established between quadrats. This approach reduced the chance of treating tillers of the same specimen in two different treatment plots.

Raillard (1992) observed that muskoxen do not graze at ground level. The lower section of grazed shoots remained intact, 1.0 to 3.0 cm above-ground. To simulate grazing by muskoxen, I followed Raillard's (1992) arbitrary measure of 1.5 cm. However, I clipped each quadrat above moss level to avoid the risk of killing the plants because the apical meristem (region from where the leaves are produced) is located below moss level (Archer and Tieszen 1980). I clipped vegetation with hand held scissors (0.2 cm blade width). To maintain a constant clipping height, I glued a 1.3 cm piece of PVC tubing underneath the scissor's blade. Following each treatment, clipped portions of sedges were removed from the plot to simulate removal of vegetation by grazing, but not saved. At the end of the experiments (5-13 August), sedges within each treated quadrat were clipped to moss level (Archer and Tieszen 1983; Chapin 1980b; Chapin and Shaver 1985)

In the laboratory, I sorted live from attached dead portion of sedges from all samples. Other plant groups such as grasses, forbs, shrubs, as well as moss and litter were removed from each sample and not considered in the analyses. After sorting, the biomass was oven-dried at 60^{0}C for 48 hrs and weighed (± 0.001 g) (Brizuela *et al.* 1986) before silica and nitrogen concentrations were measured.

3.2.4. Analyses of Plant Samples

3.2.4.1. Preparation of Samples

I washed the live biomass of each sample with 1 l of distilled water in a #325 mesh size sieve before analyzing for silica (Jones and Milne 1963; Brizuela *et al* 1986). This reduced contamination by silicon particles on the external surface of the

plant (Brizuela *et al.* 1986; Wallace *et al.* 1976). I dried (60^{0}C for 24 hrs) and then ground the samples with a Wiley mill (#30 mesh size).

3.2.4.2. Compensatory Growth of Sedges

I determined the effects of different timing and frequencies of clipping on sedges by calculating daily above-ground productivity. I divided the final biomass of each treated sample by the number of days, from the time sedges were clipped to the time of final harvest. The daily above-ground productivity of control samples was measured by estimating 21 June (snow melt) to be the start of the growing season.

3.2.4.3. Silica Analysis

I used a modifed version of the gravimetric procedure (dry ashing) to determine the silica concentration of sedges as published by Adatia and Besford (1986) (Tom Helmer pers. comm. 1994. Agriculture Canada Research Station, Agassiz, British Columbia, Canada). The procedure consisted of ashing a minimum of 1.0 g of oven-dried biomass in a 550^{0}C oven for 48 hrs using a porcelain crucible. Samples were removed from the oven and cooled to room temperature. Five ml of 0.1 N HCl was added to each crucible and placed on a hot plate in a fumehood until the HCl has evaporated to near dryness. Then, an additional 5.0 ml of 0.1 N HCl was added to the crucible and warmed until the salts had dissolved. Contents of the crucible were filtered with Whattman's #42 ashless paper and washed with hot distilled water. The filter paper was placed back in its own crucible and ashed again for 24 hrs at 550^{0}C. Samples were analyzed in duplicates. Silica concentrations were taken to be the weight of the insoluble ash expressed as a percentage of the initial sample weight.

3.2.4.4. Nitrogen Analysis

I analyzed each sample of biomass for nitrogen with a LECO analyzer (model FP-428). This required only 0.1 g of plant material and fewer steps to complete the procedure, as opposed to the conventional Kjeldahl technique (A.A.O.C. 1985). All samples were analyzed in duplicates.

3.2.5. STATISTICAL ANALYSES

3.2.5.1. Seasonal Changes of Above-Ground Biomass, Silica and Nitrogen

I tested the above-ground biomass data for normality and homogeneity of variances using the Shapiro Wilk's and Levene's tests, respectively (Milliken and Johnson 1984). All biomass estimates, and seasonal changes of silica and nitrogen were log transformed before statistical analyses. Subsequently, two-way analyses of variance (ANOVA) were performed in which the factor "site" was considered random. A multiple comparison of means using the Bonferroni method was performed when significant differences were found with two-way ANOVAs. A simple regression was used to determine the relationship between silica concentrations and time when sedges were harvested. All statistical analyses were performed with SAS software (SAS 1988).

3.2.5.2. Defoliation Experiments (Timing and Frequency)

I determined the effects of clipping on the above-ground biomass, silica and nitrogen concentrations of sedges for the timing and frequency experiments using a randomized block design. The analyses included the effects of site (*i.e.* block; random factor), treatment (fixed factor), and interaction effect (sites *x* treatments). The test of normality and homogeneity of variances was done using the Shapiro Wilk's and Levene's test, respectively. Data were log transformed, unless otherwise stated, when

either the distribution was not normal or the variances were not homogeneous. Comparisons among means were done by the Bonferroni method, only if significant differences were found among treatments.

As previously mentioned, Site 3 was naturally flooded between 28 June and 16 July, thus quadrats were not clipped on 7 July because they were underwater. This caused a 10-d "shift" in the frequency experiment (*i.e.*, sedges could not be clipped a fourth time). As a result, Site 3 was omitted from the analyses that included Sites 1 and 2. The detection of a treatment effect at Site 3 was determined by a one-way ANOVA.

3.2.5.3. Timing versus Frequency of Clipping

An alternate approach was considered to determine whether clipping would increase above-ground productivity, silica and nitrogen concentrations of sedges. I used a randomized block design to analyze comparisons between sedges clipped once and those clipped at different frequencies. For Sites 1 and 2, three comparisons were made between sedges: 1) clipped once (7 July) *versus* clipped twice (27 June and 7 July); 2) clipped once (17 July) *versus* clipped three times (27 June, 7 July and 17 July); and 3) clipped once (27 July) *versus* clipped four times (27 June, 7 July, 17 July and 27 July). However, the flooding of Site 3 caused only two comparisons to be analyzed; 1) clipped once (17 July) *versus* clipped twice (27 June and 7 July); and 2) clipped once (27 July) *versus* clipped three times (27 June, 17 July and 27 July).

3.2.5.4. Regression Analyses

A simple regression was used to determine the relationship between the seasonal concentration of silica (digestibility reducing agent), and nitrogen (index of plant quality). Using multiple regression, I analyzed the silica concentration with time (Julian days) and nitrogen. Furthermore, simple regressions were used to determine

the relationship between silica and nitrogen when sedges were either clipped once at different times or frequently during the growing season.

3.2.5.5. Repeatability Test (Hotelling's T^2 Test)

In the laboratory, samples used for determining silica concentrations were not selected randomly before each analysis. Due to the great number of samples (220 in duplicates), the approach was systematic: analyses were done in sequence, on samples with a different treament each time. To confirm the validity of the results without randomization, I performed a repeatability test of samples. Differences between sites and dates of collection were controlled for with this type of analysis because each sample was considered a "block". In all, 18 samples from the "seasonal changes" (17 July, 27 July or 5-13 August) were selected for repeatability measures. Each sample was either divided into two or three sub-samples, depending on the amount of plant material left for the analyses. In the analysis, each group of sub-samples was referred as a "set". The first two sets were analyzed with 1.4 g of plant material. I consistently used equal amount of plant material to minimize the variance among samples. An additional 9 samples were examined in a third set, also with 1.4 g of plant material.

During the 2 months of analysis, the acid solutions and oven used in the gravimetric procedure differed between some dates of analysis. For this reason, I analyzed sets 1 and 2 with the same acid solution and oven while a different solution of acid and oven were used for set 3. Three different comparisons (*i.e.*, set 1 *versus* 2; set 1 *versus* 3; and set 2 *versus* 3) were analyzed with Hotelling's T^2 Test (SAS 1988).

3.3. RESULTS

3.3.1. Seasonal Changes in Above-Ground Biomass

Sedges in meadows became increasingly available to muskoxen as the season progressed, as significant differences in above-ground biomass were found between sampling dates ($F = 60.34$, $P < 0.002$; Fig. 3.3.a). At Site 1, the biomass of sedges on 27 June increased on average by 46% every 10-d of growth. By 27 July, sedges tripled their biomass and peaked at 23.04 ± 2.40 g m^{-2} (S.E.), but decreased by 9% on the last sampling date (5-13 August). Seasonal changes in biomass of sedges from Site 3 followed a similar trend as sedges from Site 1. On 27 July, the biomass of sedges peaked at 26.54 ± 4.56 g m^{-2} (S.E.), 3.8 times greater than their initial biomass, but also decreased (7%) on the last sampling date. In contrast, biomass at Site 2 peaked at the end of the sampling period (5-13 August) at 22.64 ± 1.58 g m^{-2} (S.E.), being 4.7 times greater than the initial biomass. The above-ground biomass of sedges was significantly different between all three sedge meadows ($F = 4.94$, $p = 0.04$).

3.3.2. Seasonal Changes in Silica

Silica concentration in sedges generally increased throughout the season (Fig. 3.3b). Silica concentration varied significantly between sampling dates ($F = 29.95$, $p < 0.001$), but not between sites ($F = 1.67$, $p = 0.25$). At the beginning of the growing season (27 June), the mean silica concentration of sedges for the three sites increased an average of 17% every 10-d until 17 July. However on 27 July the silica concentration in sedges decreased by 18%. Silica concentration peaked late in the season (5-13 August) reaching 1.55 ± 0.05% (S.E.). The mean silica concentration of sedges on 5-13 August was significantly different from all other dates (multiple comparisons). During the sampling period (27 June to 5-13 August), silica concentration in sedges increased by a factor of 1.8. The relationship between silica

and time (*i.e.*, sampling dates) was determined by a simple regression ($F = 41.53$, $p < 0.001$; silica = -1.93 + 0.02 time (days), $r^2 = 0.37$).

3.3.3. Seasonal Changes in Nitrogen

There was a significant interaction between sites and sampling dates ($F = 5.90$, $p < 0.001$; Fig. 3.3c). This interaction was seen in the different trends of nitrogen concentrations during the sampling period between Site 3 and Sites 1 and 2. At Site 3, nitrogen concentration increased 28% by 27 July. On 5-13 August, nitrogen concentrations had decreased by 18%. In contrast, the highest concentration of nitrogen at Sites 1 and 2 was reached two weeks earlier than at Site 3 (7 July), and decreased by 24% and 15%, respectively, thereafter until the last sampling date (5-13 August).

3.3.4. Defoliation Experiments

A) Timing of Clipping

The daily above-ground productivity of sedges clipped once was not significantly different from that of controls ($F = 0.95$, $p = 0.49$; Fig. 3.4a). In other words, sedges clipped once produced, on a daily basis, the same amount of plant material as controls. This response was observed regardless of when sedges were clipped during the sampling period. However, trends showed that sedges from Sites 1 and 2 increased their daily above-ground productivity by 50% and 53%, respectively, between 27 June and 27 July. In contrast, sedges from Site 3 decreased their productivity by 24% during the same period.

Clipping sedges once, at any time during the season, did not promote significant changes in silica concentration ($F = 1.27$, $p = 0.37$; Fig. 3.4b). At Sites 1 and 3, silica concentration in sedges peaked by 17 July. At this time, the silica

concentration was 24% (Site 1) and 26% (Site 3) greater than unclipped sedges. In contrast, silica concentrations at Site 2 did not show a strong seasonal trend during the sampling period.

Although productivity and silica concentration were not significantly affected by a single clipping, nitrogen concentration in sedges responded positively to such a treament ($F = 7.90$, $p = 0.01$). However, the clipping effect generally decreased throughout the season for all three sites (Fig. 3.4c). Furthermore, significant differences were found between the three sites ($F = 43.92$, $p < 0.001$). At Site 3, nitrogen concentration of sedges clipped on 27 June was 16% greater than untreated sedges which decreased thereafter by 6% until 27 July. Nitrogen concentration in sedges from Site 3, clipped on 27 June, was 21% and 17% greater than sedges from Sites 1 and 2, respectively.

B) Effects of Clipping Frequency

Similar to when sedges were clipped once at different time intervals, frequency of clipping did not significantly affect the daily above-ground productivity of sedges. Sedges from Sites 1 and 2 had the same growth rate as controls ($F = 6.34$, $p = 0.08$; Fig. 3.5a). The same clipping response was found for sedges from Site 3 ($F = 0.84$, $p = 0.45$; Fig. 3.6a). At Sites 1 and 2, a trend showed that the productivity of sedges increased as the frequency of clipping increased from 7 July to 27 July (Site 1 = 18%; Site 2 = 40%). In contrast, sedges from Site 3 decreased in productivity when clipping frequency increased.

Silica concentration of sedges from Sites 1 and 2 was not altered by the three different clipping frequencies ($F = 0.82$, $p = 0.56$; Fig.3.5b); however, the silica concentration increased as the frequency of clipping increased only for sedges from Site 1. Although showing a strong trend, sedges from Site 3 did not significantly increase their silica concentration as a result of two or three clippings ($F = 2.78$,

$p = 0.09$; Fig. 3.6b).

There was no significant clipping effect on the nitrogen concentration in sedges from Sites 1 and 2 ($F = 2.53$, $p = 0.23$; Fig. 3.5c). In contrast, sedges from Site 3 significantly increased their nitrogen concentration by 21% and 23% more than untreated sedges when clipped two and three times, respectively ($F = 30.35$, $p < 0.001$; Fig. 3.6c). Multiple comparisons established no difference between these two clipping frequencies.

3.3.5. Timing versus Frequency of Clipping

I compared the daily above-ground productivity of sedges (Sites 1 and 2) clipped once at different times during the growing season to those clipped frequently (two, three or four times; Fig. 3.7). Above-ground productivity was not significantly different among treatments (Table 3.2a), or between sites ($p > 0.41$). Similarly, treatments did not significantly alter the silica and nitrogen concentrations for all three comparisons (Figs. 3.8 & 3.9; Table 3.2a). Silica and nitrogen concentrations increased when sedges were clipped twice and four times *versus* once.

At Site 3, above-ground productivity significantly increased in response to three clippings relative to the single clipping treatment (Fig. 3.10; Table 3.2.b). The response of sedges clipped twice followed the same trend but the difference was not significant. Silica concentrations decreased when sedges were clipped twice as opposed to once, but significantly increased when clipped more frequently. On the other hand, nitrogen concentrations of sedges were significantly increased by both frequencies of clipping (Fig. 3.10; Table 3.2.b).

3.3.6. Regression Analyses (Silica versus Nitrogen)

A simple regression determined that the seasonal variation in nitrogen concentrations was negatively related to silica concentrations in sedges (F = 10.62, $p < 0.002$; silica = 2.25 + -0.40 nitrogen; $r^2 = 0.13$). When nitrogen and time were analyzed in a multiple regression, the slope was also significantly different from zero (F = 23.63, $p < 0.001$). Silica was positively related to time and negatively to nitrogen (silica = 0.01 time (days) + (- 0.22) nitrogen; $r^2 = 0.40$).

When sedges were clipped once at four different times, the relationship between silica and nitrogen was not significant (F = 3.73, p = 0.06). In contrast, a significant positive relationship existed when sedges from Sites 1 and 2 were clipped at different frequencies (F = 4.95, p = 0.03; silica = 0.88 nitrogen, $r^2 = 0.13$). However, when sedges from Site 3 were frequently clipped, silica and nitrogen concentrations were not related (F = 0.29, p = 0.60).

3.3.7. Repeatability Test (Hotelling's T^2-Test)

I assessed the repeatability of the gravimetric procedure for silica by comparing three sets of samples (Table 3.3). In the first comparison (set 1 *versus* set 2), samples (n = 18) were analyzed for their silica concentration using the same acid solution and oven. The silica concentration was found to be different between the sets (F = 20.91, $p < 0.001$). In the second comparison (set 2 *versus* set 3), samples (n = 9) were analyzed with different acid solutions and ovens. There was also a significant difference in silica concentration between these sets (F = 44.40, $p < 0.001$). However, no difference (F = 0.02, p = 0.89) was determined between sets 1 and 3 (9 samples).

3.4. DISCUSSION

3.4.1. Seasonal Changes in Above-Ground Biomass

In the Arctic, the availability of forage to muskoxen decreases with increasing latitude, and the associated reduction of the growing season (Klein and Bay 1990). Above-ground biomass of sedges in the vicinity of Cambridge Bay, Victoria Island (69^0 N) was expected to be greater than the net production found at higher latitudes. Such was not the case; the net production of sedges averaged 25 g m^{-2} as opposed to 23 g m^{-2} in northern Greenland (82^0 N) and 26 g m^{-2} on Ellesmere Island (78^0 N) (Henry and Svoboda 1994; Klein and Bay 1990). The low productivity of sites sampled near Cambridge Bay may be explained by: 1) small grazing pressure by muskoxen (Henry *et al.* 1986), which did not increase the net production of sedge meadows as opposed to heavily grazed sites (Henry and Svoboda 1994) and/or, 2) sedges responding to different environmental factors (see Chapin and Shaver 1985; McNaughton 1979a). Also, the biomass of sedges was underestimated in this study because sedges were clipped at moss level as opposed to ground level.

3.4.2. Seasonal Changes in Silica

Past studies have found silica concentration of sedges and grasses to either increase (Bezeau *et al.* 1966; Gali and Smith 1992; Handreck and Jones 1968) or decrease (McNaughton *et al.* 1985) during the growing season. In the present study, silica concentration of arctic sedges increased during the sampling period (27 June 5-13 August), with the exception of a decrease on 27 July. Different growth stages of sedges may account for this trend. Bezeau *et al.* (1966) found that silica concentration of sedges in mixed prairies decreased during the second stage of growth and recovered as the season progressed. However, the decline may simply be a sampling artifact due to small sample size (n = 5, per site, per sampling date) and small quantities of plant material (1-2 g) analyzed. Also, samples from each sampling date were not

randomized when the analyses were performed. Analyses were done systematically (*i.e.*, all samples of one sampling date at a time).

3.4.3. Seasonal Changes in Nitrogen

Seasonal changes in nitrogen content of sedges (*i.e.*, early season increase followed by a decrease as the season progressed) were consistent with previous studies (Chapin *et al.* 1975; Chapin 1980a; Chapin *et al.* 1980; Ouellet 1992). However, nitrogen concentration of sedges from Site 3 was different possibly due to the flooding, and followed the seasonal increase in biomass of sedges. Because these seasonal changes in nitrogen were site specific, this suggests that muskoxen may encounter sedges of high quality during most of the growing season.

3.4.4. Defoliation Experiments

A) Timing of Clipping

Daily above-ground productivity of sedges was not altered when clipped once at different times during the sampling period. Growth rates were similar between clipped and control sedges. Therefore, I concluded that clipped sedges did not compensate for their loss of biomass, contrary to Ouellet's (1992) and Raillard's (1992) findings. Based on previous results of compensation by plants, Owen and Wiegert (1981) suggested that a mutualistic relationship exists between grasses and grazers. In contrast, my results dispute the occurrence of such a relationship because sedges did not benefit from being clipped (*i.e.*, no compensation). However, because growth rates of clipped sedges were not significantly affected when leaf material was removed, sedges were tolerant to clipping.

Silica concentrations were not significantly modified when sedges were clipped once at different times during the sampling period. This outcome was different from

previous findings that either reported an increase (McNaughton and Tarrants 1983; McNaughton *et al.* 1985) or a decrease (Brizuela *et al.* 1986; Cid *et al.* 1989; Cid *et al.* 1985) in silica concentration in response to artificial defoliation. Although silica responses in this experiment were not significant, trends were observed for Sites 1 and 3. Silica concentration of sedges increased progressively between the first and third sampling date (Fig. 3.4b). Lanning *et al.* (1958) proposed that a positive relationship exists between the amount of silica and water that a plant absorbs. During the sampling period I observed important differences in water availability between sites (Site 3 > 1 > 2). I predicted that silica concentrations would decrease from Sites 3, 1 and 2. Such a trend was only observed in sedges clipped on 27 June and 17 July, which does not strongly support the relationship between silica and water availability.

Nitrogen concentration of sedges was increased by a single clipping. Effects of this treatment were more notable when sedges were clipped in the early stages of growth. The positive response of sedges to clipping suggests that a redistribution of nitrogen to the new growth occurred, made possible by either an increased root uptake or mobilization from underground storage organs (Raillard 1992). Other studies have confirmed this effect of clipping either in artificial (Ouellet 1992; Raillard 1992) or natural (Cargill and Jefferies 1984; Zellmer *et al.*, 1993) defoliation experiments.

B) Clipping Frequency

No compensatory growth was found at any of the three sites when sedges were clipped frequently (*i.e.* two, three or four times). Therefore, this result opposes the herbivore optimization model (McNaughton 1979b). However, productivity of sedges from Sites 1 and 2 tended to increase as the frequency of clipping increased, which would suggest that compensation could be achieved.

Although the silica concentration of sedges was not significantly affected by different clipping frequencies, a trend was observed at Site 1. Silica concentrations

tended to increase, above control levels, with each treatment (*i.e.* from two, to three, to four clippings). This suggests that silica concentrations may be increased by multiple clippings, but the effect appears to be site specific since no trends were observed at Sites 2 and 3.

An important point was raised by O'Reagain and Mentis (1989) in their review on leaf silicification in grasses that was not addressed by McNaughton *et al.* (1985). O'Reagain and Mentis (1989) proposed that the significant difference observed in the silica concentration of the Serengeti grasses may simply have been caused by an increase in transpiration from the cut surface of the leaf. In other words, the increase may not have been a "true" response by the grasses to actively promote their silica uptake. Even if the increase in silica concentration of grasses from the Serengeti is a real response to herbivory, whether or not this increase is biologically significant remains to be addressed. Predictably, muskoxen should not be deterred from grazing arctic sedges due to the low concentrations (*ca.* 1.5%) of silica. These relatively low concentrations are likely a consequence of the soil solubility reduced by freezing and the short growing season (Sangster and Hodson 1986). In contrast, Gali-Muhtasib *et al.* (1992) determined that prairie voles (*Microtus ochrogaster*) decreased their consumption of grasses grown with silica. They concluded from their experiments that silica could act as a grazing deterrent against vertebrate herbivores. A further investigation could be conducted with captive muskoxen to determine the extent to which palatability and digestibility are affected by different concentrations of silica. This study could determine the minimum concentration of silica which would significantly reduce a muskoxen's nutritional gain from foraging on sedges. Consequently, the study would indicate whether the low concentrations of silica found in arctic sedges are likely to affect muskoxen.

In contrast to other studies (Chapin 1980a&b; Ouellet 1992; Raillard 1992), multiple clippings did not significantly affect the nitrogen concentration of sedges at Sites 1 and 2. However, nitrogen concentration of sedges from Site 3 increased

significantly to treatments of two and three clippings. We can conclude that heavy grazing by muskoxen would improve sedge quality, more so in wet than in mesic meadows. Muskoxen would therefore benefit from this increased quality of forage during fall and early winter, when they regain most of their annual body weight and fat before the rutting period (White *et al.* 1989).

3.4.5. Timing versus Frequency of Clipping

Comparisons between the different timing and frequency of clipping confirmed that simulated grazing by muskoxen did not have any effects on the productivity, silica and nitrogen concentrations in sedges from mesic meadows (Sites 1 and 2). However, changes in productivity and in silica and nitrogen concentrations were detected in sedges from a wet meadow (Site 3 was naturally flooded during the summer). This suggests that the effects of clipping were produced in conjuntion with an increase in soil moisture at Site 3. As well, the frequency at which a muskoxen graze appears to influence the productivity, silica and nitrogen concentrations of sedges in a wet meadow more so than in mesic meadows.

3.4.6. Silica versus Nitrogen

Previous studies found an inverse relationship between silica and nitrogen (Wallace *et al.* 1976; Wallace 1989). Arctic sedges also increased their silica concentration while nitrogen content decreased over the growing season. At the end of the season (5-13 August), silica concentration was highest while nitrogen concentration in sedges was lowest. Thus, muskoxen may be expected to feed more intensively early in the growing season and benefit from the low silica and high nitrogen concentration in sedges. However, graminoids composed only 13% of rumens of muskoxen in early summer (27 June) as opposed to 39% in late August (Thing 1984).

After a single clipping, silica and nitrogen concentrations were affected independently by the treatment (*i.e.*, no relationship existed). However, when sedges were clipped at increased frequencies both silica and nitrogen concentration of sedges from Site 1 and 2 increased. Since silica and nitrogen have been shown to vary temporally and spatially, muskoxen should be able to select the most nutritious sedges while avoiding high silica content. Muskoxen may be able to achieve this by processing information about sedges through two interrelated systems: affective (postingestive feedback using taste) and cognitive (preingestive feedback using sight and smell; Provenza *et al.*, 1992), and therefore avoid the problems associated with ingesting silica.

3.4.7. Repeatability Test

The gravimetric procedure was unable to determine the same concentration of silica between three sets of the same samples, two times out of three. Statistically, differences were found between sets, however biologically such differences may mean very little to muskoxen. Small amounts of plant material (1.4 g) used in the procedure may have accounted for the differences betweens sets; differences in silica concentration when analyzing small amounts of plant material are greater than if the same differences were present in larger amounts of plant material. Weighing of samples (hot) may also have contributed to the differences observed. To alleviate the problem, a similar test using a greater sample size and amount of plant material (> 5 g) should be repeated and presented in future studies to determine the validity of silica values reported.

Silica values from this study may be refuted because of the lack of repeatability from the gravimetric procedure. I believe these values should be interpreted with caution but not refuted. No other studies that have used the gravimetric procedure to determine silica values in plants has presented results of such a test (Van Der Vorm 1980; Adatia and Besford 1986; Menzies *et al.* 1991).

Before using the gravimetric procedure, I analyzed some plant samples for silica using a modification of the colorimetric procedure (Grimshaw *et al.* 1989) since a similar technique was used in african (McNaughton and Tarrants 1983; McNaughton *et al.* 1985) and north american studies (Brizuela *et al.* 1986; Cid *et al.* 1989; Cid *et al.* 1990). When I performed this technique I was either unable to get a reading on the spectrophotometer or the duplicates of samples were inconsistent. A possible explanation for these problems may be the use of multiple steps and reagents with this procedure, thus increasing the chances of committing errors.

I concluded from using the gravimetric and colorimetric procedures that both techniques of silica determination were not without problems. However, past studies (McNaughton and Tarrants 1983; Cid 1985; McNaughton *et al.* 1985; Brizuela *et al.* 1986; Cid *et al.* 1989; Cid *et al.*1990) have made conclusions without being critical about the procedure used for silica analysis, and have never been criticized for doing so. Failing to acknowledge such limitations in published experiments jeopardizes the validity of the findings. A more rigorous description of how samples were analyzed for silica, beyond simply mentioning which technique was used, should be presented. By doing so, questions about the validity of the results and conclusions would be clarified.

I argue that presenting evidence of a technique's limitations is an essential component of the study which gives the ability to assess whether the technique is acceptable or not. Without this information conclusions of any experiments are suspect. The need to clarify the potential problems of using a technique for silica determination should be a priority for future studies.

3.5. CONCLUSIONS

1) No compensatory growth of sedges resulted from the timing and frequency experiments.

2) Silica concentrations increased over the growing season but were not altered by any clipping treatments.

3) Nitrogen concentrations were primarily high in early growing season and decreased over time. Timing and frequency of clipping increased nitrogen concentrations at Site 3.

4) Clipping effects were more prevalent for sedges at Site 3 (flooded between 28 June and 16 July) than at Sites 1 and 2.

5) Silica increased as the nitrogen concentrations decreased over time in unclipped sedges.

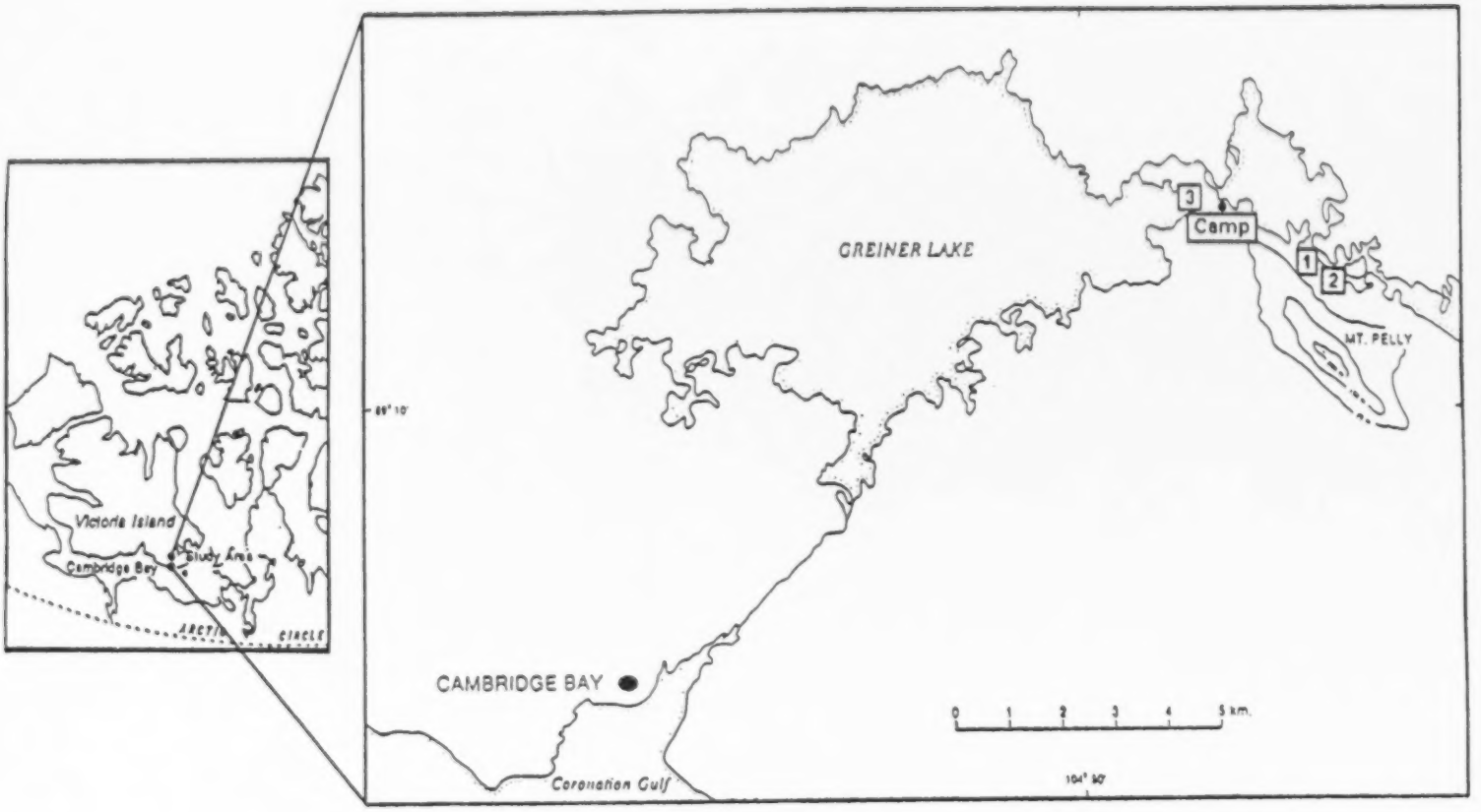

Figure 3.1. Location of base camp (69° 12' N, 104° 46' W) and three sampling sites established in summer of 1992.

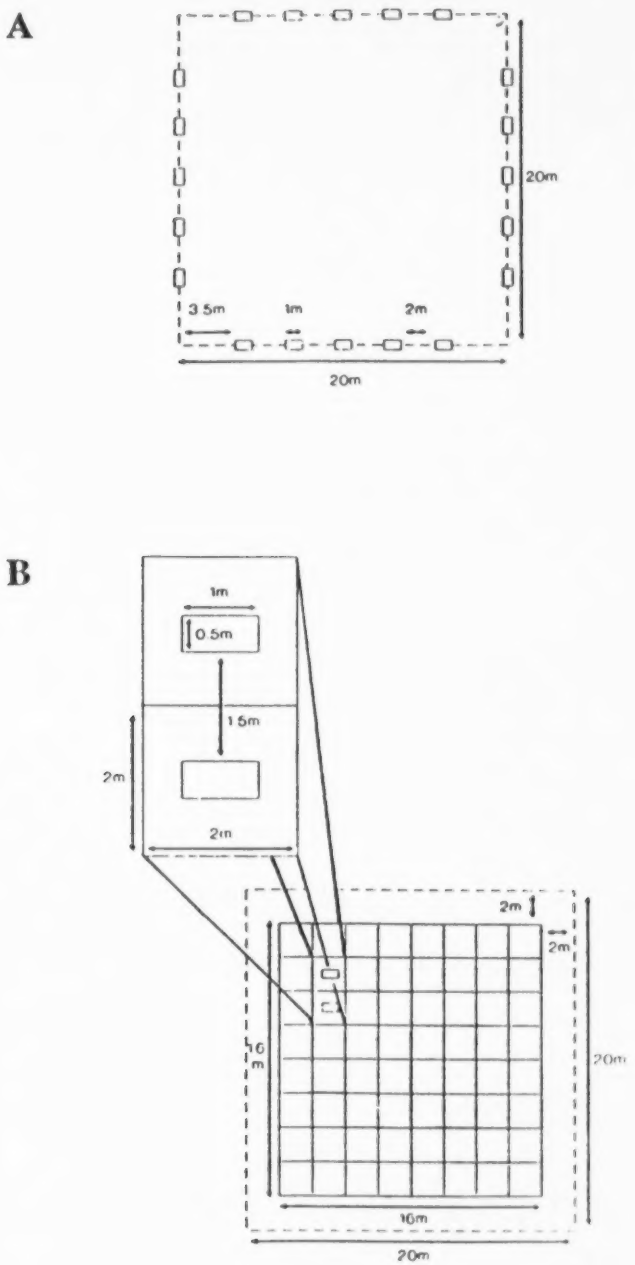

Figure 3.2. Sampling design for determining A) seasonal changes and B) effects of clipping on above-ground live productivity, silica and nitrogen concentrations of sedges. Quadrats are depicted by rectangles and are 1.0 m x 0.5 m in size.

Table 3.1. Summary of the treatments for the defoliation experiments. The field codes indicate when and how frequently sedges from a quadrat were clipped. Sedges from eight quadrats were treated for each of the field codes (n = 64). The sampling dates mark when sedges of these quadrats were clipped.

Field Code	Treatments Timing (T) or Frequency (F)	Sampling Dates
1	Clipped once (T)	27 June
2	Clipped once (T)	7 July
3	Clipped once (T)	17 July
4	Clipped once (T)	27 July
12	Clipped 2 times (F)	27 June & 7 July
123	Clipped 3 times (F)	27 June, 7 July & 17 July
1234	Clipped 4 times (F)	27 June, 7 July, 17 July & 27 July
C	Control	5-13 August / Final Harvest

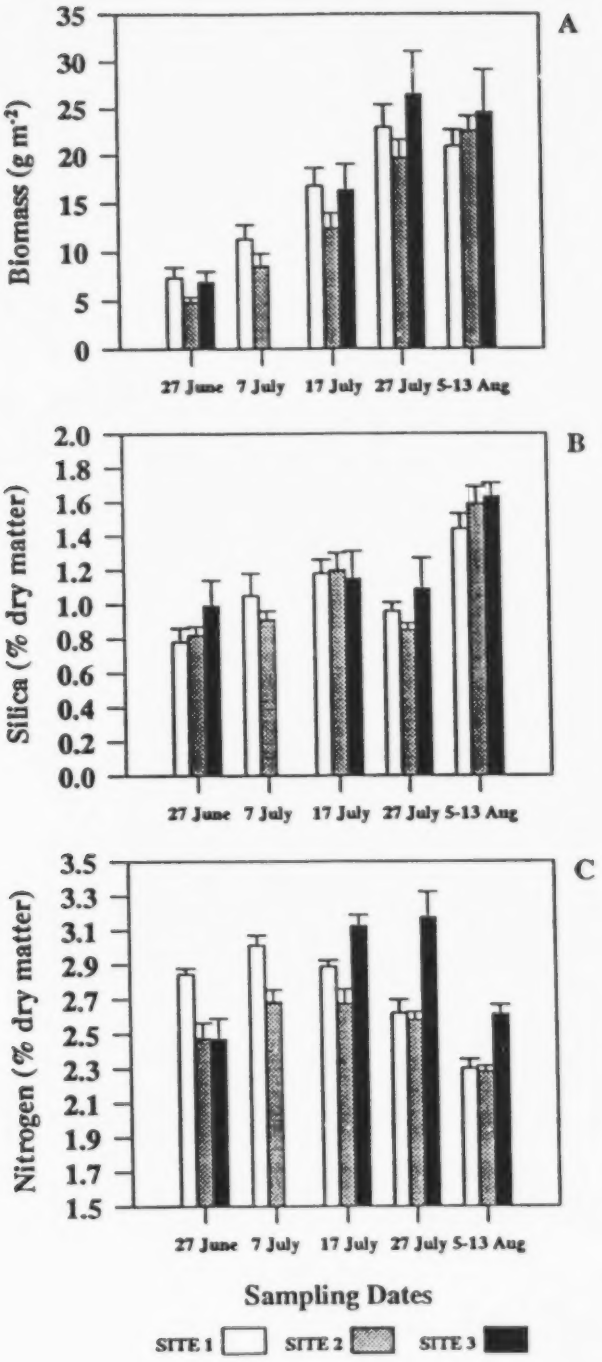

Figure 3.3. Seasonal changes in A) above-ground biomass (g m^{-2}), B) silica (% dry matter), and C) nitrogen (% dry matter) concentrations of sedges for three sites sampled. Data are means (± S.E.); n = 4-8 per sampling date.

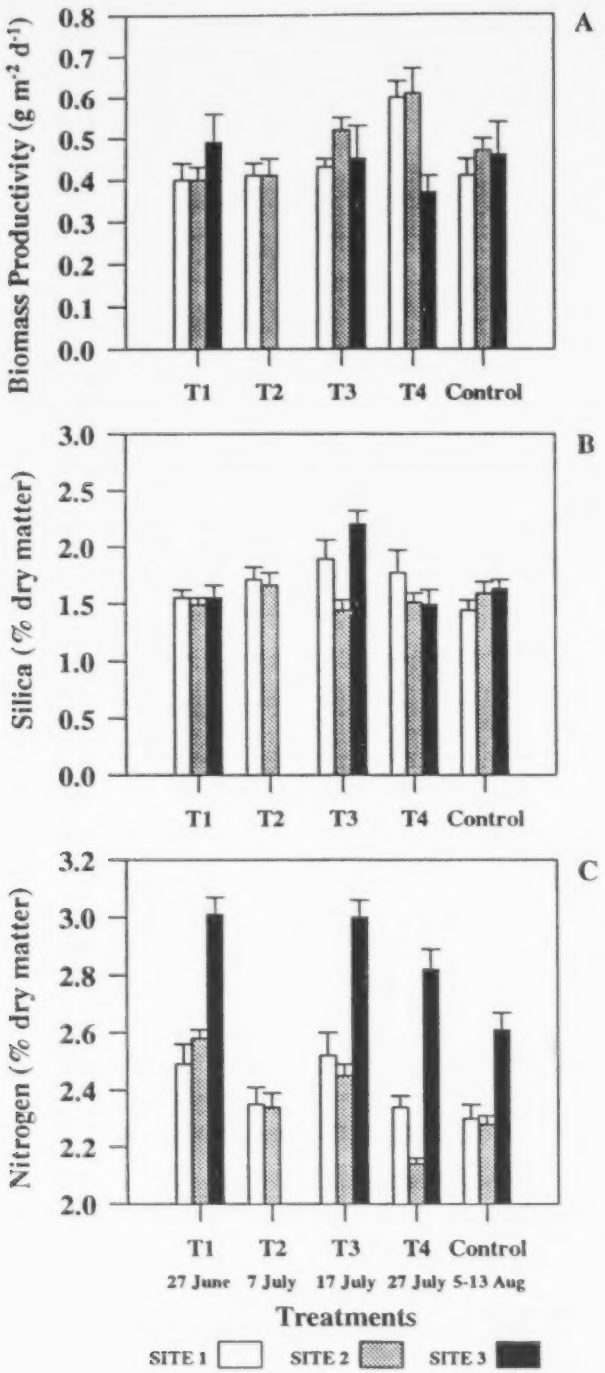

Figure 3.4. Effects of clipping once at four different times in the season (10-day intervals) on A) daily above-ground productivity (g m^{-2} d^{-1}), B) silica (% dry matter), and C) nitrogen (% dry matter) concentrations. Data are means (± S.E); n = 7-8 per treatment.

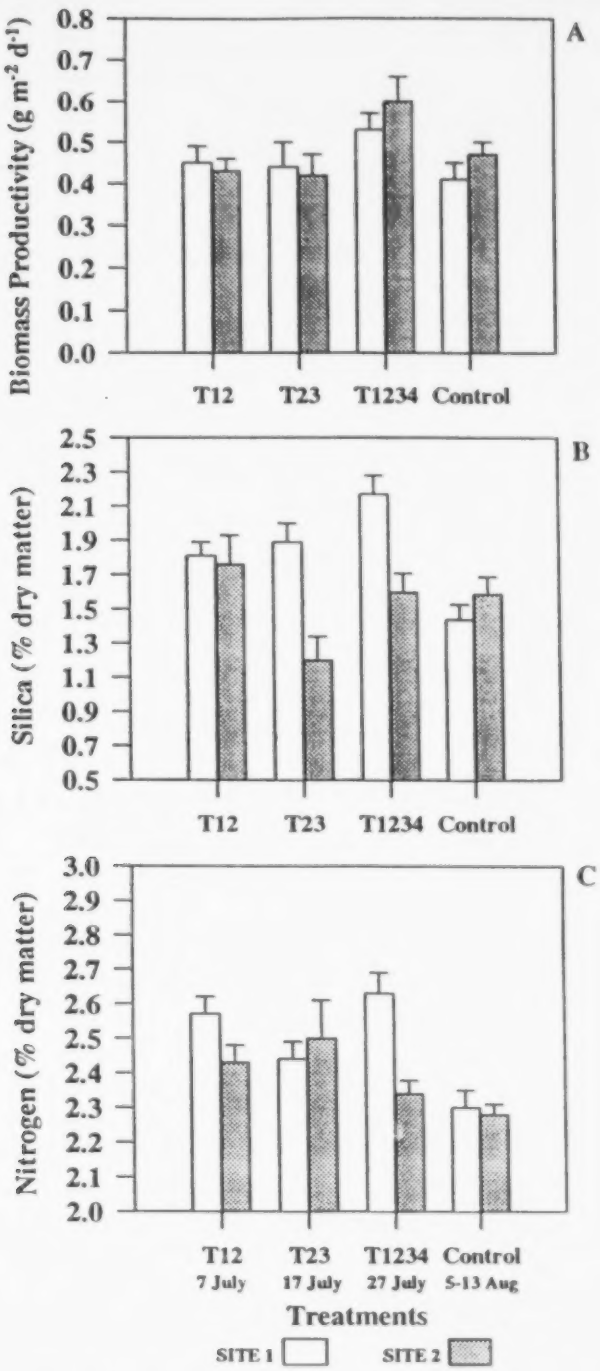

Figure 3.5. Effects of two, three or four clippings on A) daily above-ground productivity (g m^{-2} d^{-1}), B) silica (% dry matter) and C) nitrogen (% dry matter) concentrations of sedges from Sites 1 and 2 during the growing season. Data are means (± S.E); n = 4-8 per treatment.

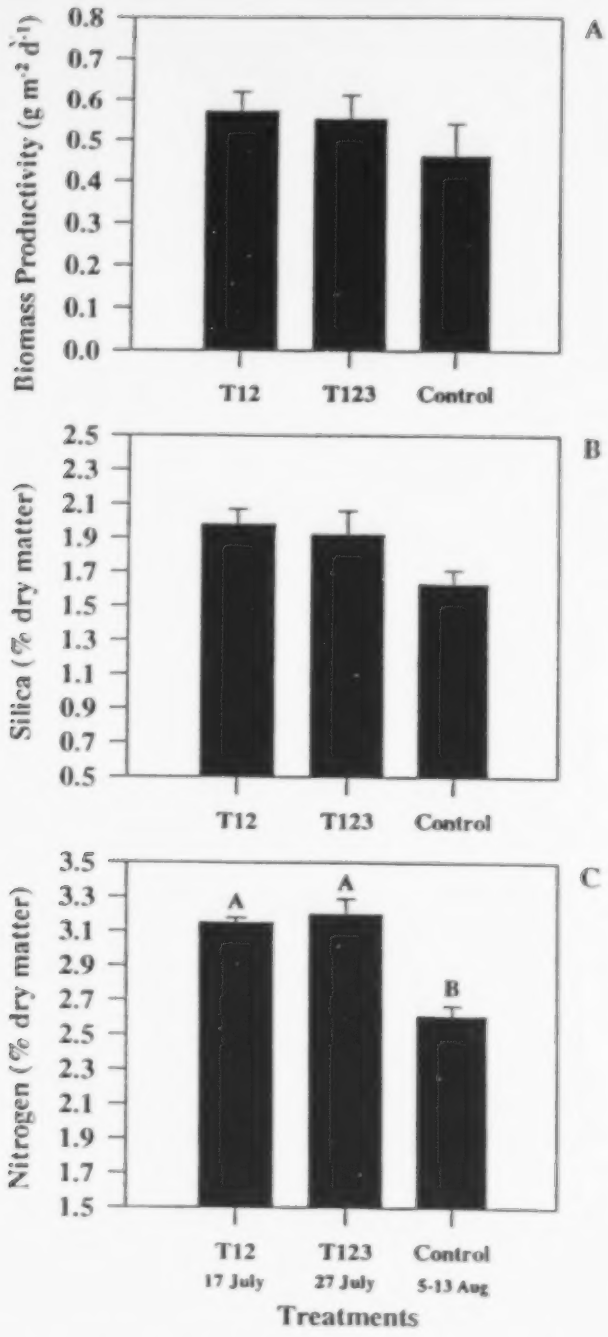

Figure 3.6. Effects of two or three clippings on A) daily above-ground productivity (g m^{-2} d^{-1}), B) silica (% dry matter) and C) nitrogen (% dry matter) concentrations of sedges from Site 3 during the growing season. Different letters indicate significant differences ($P < 0.05$). Data are means (± S.E); n = 7-8 per treatment.

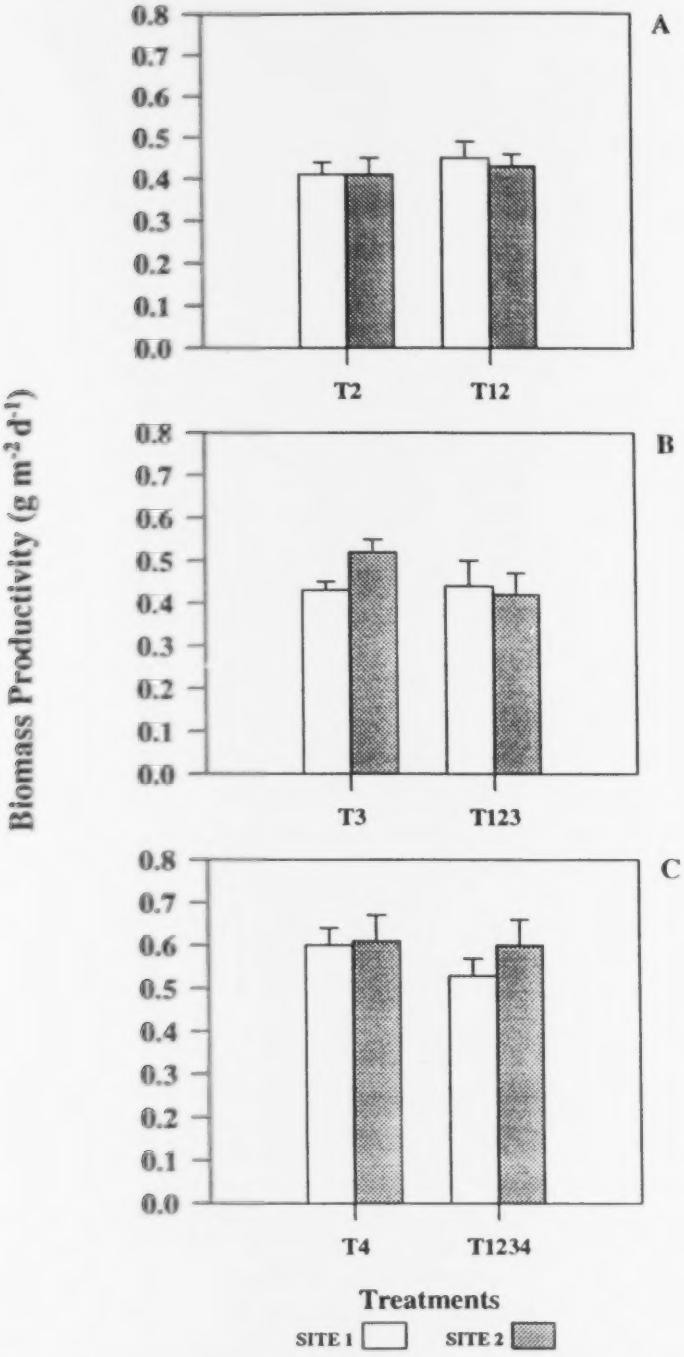

Figure 3.7. Three comparisons made between timing and frequency experiments on daily above-ground productivity (g m^{-2} d^{-1} ± S.E.) of sedges from Sites 1 and 2. Comparisons were made between sedges clipped: A) once (7 July) and twice (27 June and 7 July); B) once (17 July) and three times (27 June, 7 July and 17 July); and C) once (27 July) and four times (27 June, 7 July, 17 July and 27 July). Data are means (± S.E); n = 5-8 treatment/site.

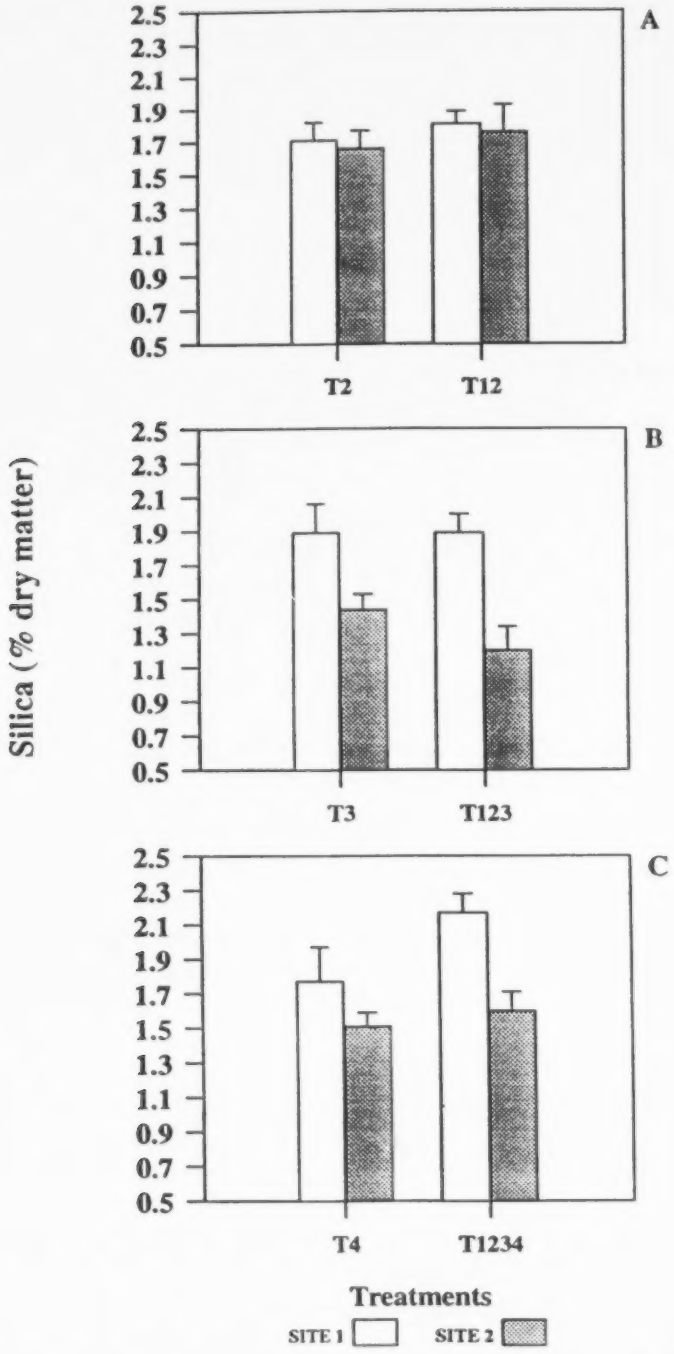

Figure 3.8. Three comparisons made between timing and frequency experiments on silica concentrations (% dry matter ± S.E.) of sedges from Sites 1 and 2. Comparisons were made between sedges clipped: A) once (7 July) and twice (27 June and 7 July); B) once (17 July) and three times (27 June, 7 July and 17 July); and C) once (27 July) and four times (27 June, 7 July,17 July and 27 July). Data are means (± S.E); n = 5-8 treatment/site.

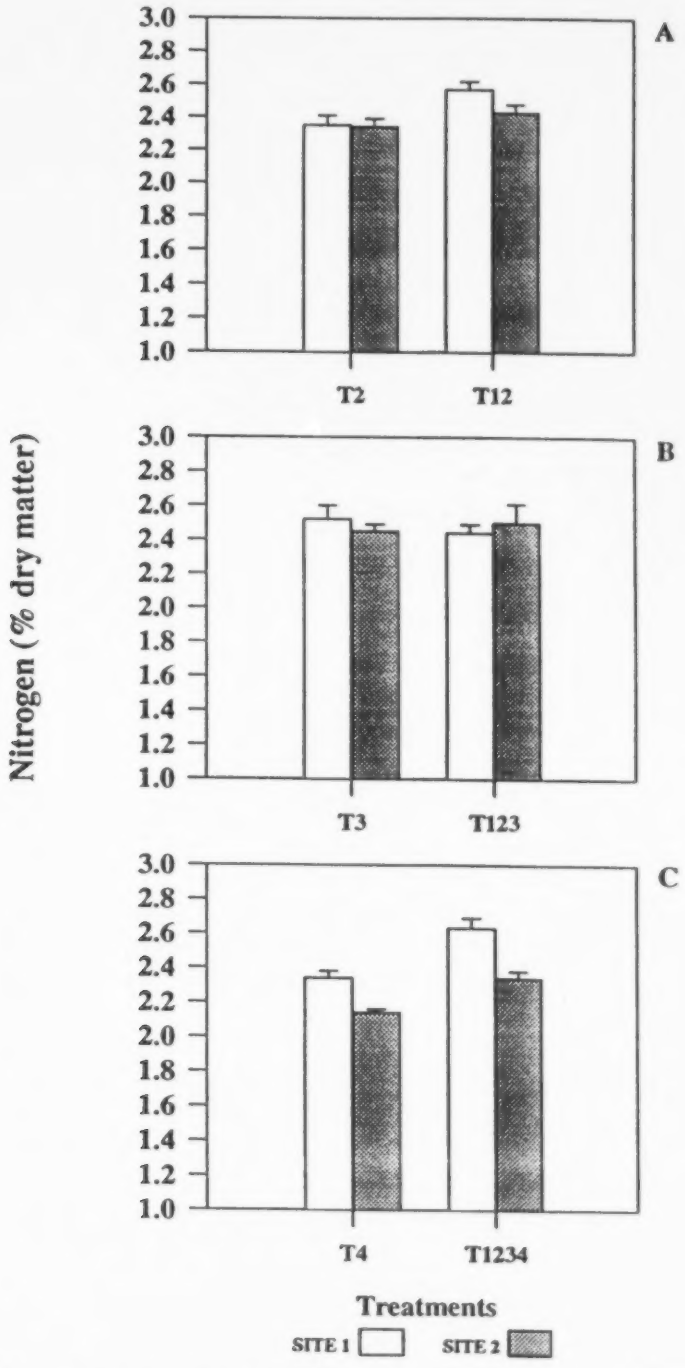

Figure 3.9. Three comparisons made between timing and frequency experiments on nitrogen concentrations (% dry matter ± S.E.) of sedges from Sites 1 and 2. Comparisons were made between sedges clipped: A) once (7 July) and twice (27 June and 7 July); B) once (17 July) and three times (27 June, 7 July and 17 July); and C) once (27 July) and four times (27 June, 7 July, 17 July and 27 July). Data are means (± S.E); n = 4-8 treatment/site.

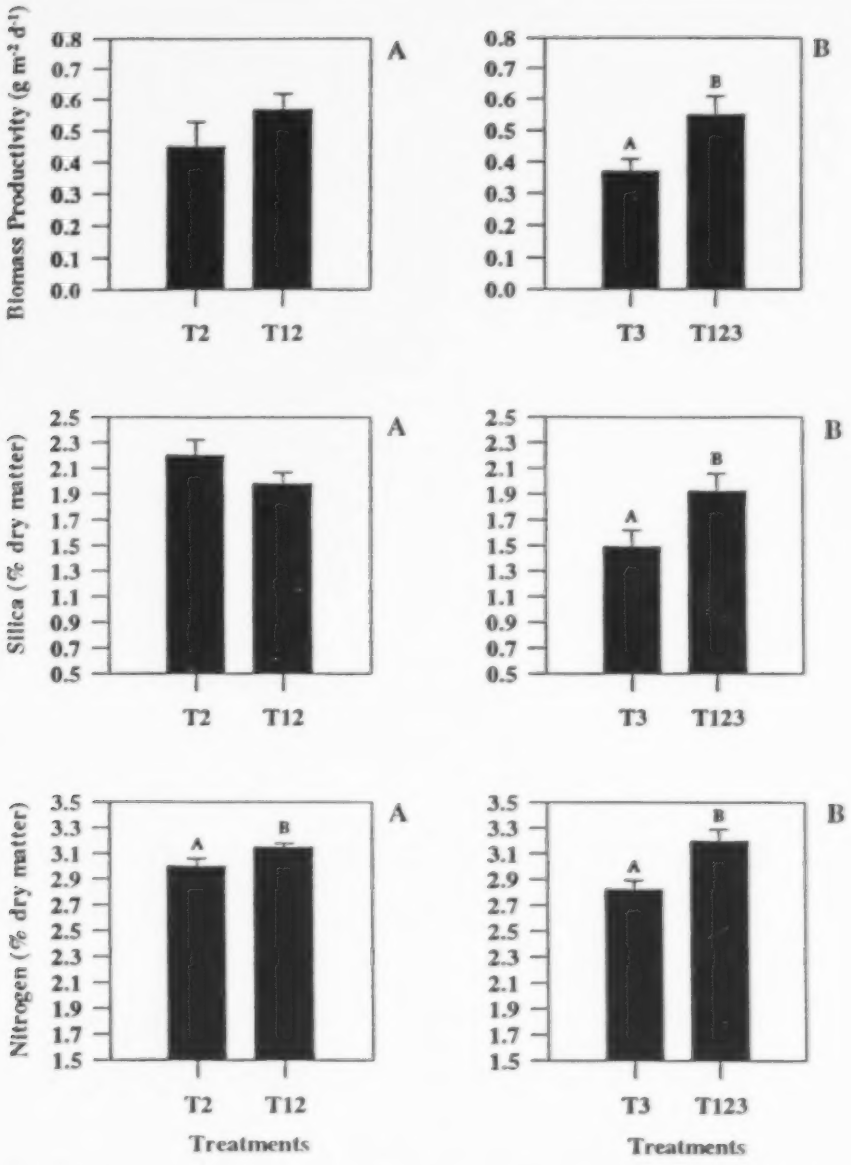

Figure 3.10. Two comparisons made between timing and frequency experiments on 1) daily above-ground productivity, 2) silica and 3) nitrogen concentrations of sedges from Site 3. Comparisons were made between sedges clipped: A) once (17 July) and twice (27 June and 17 July) and B) once (27 July) and three times (27 June, 17 July and 27 July). Different letters indicate significant differences ($P < 0.05$). Data are means (± S.E); n = 8 per treatment.

Table 3.2. Summary of the clippingeffects between the timing and frequency experiments on the productivity, silica and nitrogen concentrations of sedges for A) Sites 1 and 2, and B) Site 3. Statistical results were determined using a randomized block design.

A) SITES 1 and 2

Clipping Events	Productivity			Silica			Nitrogen		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
T2 *versus* T12	12.07	1	0.18	11.20	1	0.18	6.75	1	0.23
T3 *versus* T123	0.72	1	0.55	0.97	1	0.51	0.03	1	0.89
T4 *versus* T1234	1.14	1	0.48	2.87	1	0.34	30.32	1	0.11

B) SITE 3

Clipping Events	Productivity			Silica			Nitrogen		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
T2 *versus* T12	1.92	1	0.19	2.03	1	0.18	4.93	1	0.04
T3 *versus* T123	5.90	1	0.03	5.17	1	0.04	12.94	1	0.003

Table 3.3. Silica concentrations (% dry matter) of sedges from three sets of the same samples and the percent difference between three comparisons made were determined to assess the repeatability of the gravimetric procedure. Samples were from the "seasonality experiment" (17 July, 27 July, and 5-13 August).

SAMPLE	SET					% DIFFERENCE BETWEEN SETS		
	1	2	1	2	3	1&2	2&3	1&3
1	1.07	0.94	1.07	0.94	1.06	12.15	11.32	0.93
2	1.31	1.09	1.31	1.09	1.32	16.79	17.42	0.76
3	0.93	0.81	0.93	0.81	0.89	12.90	8.99	4.30
4	1.21	1.00	1.21	1.00	1.09	17.36	8.26	9.92
5	1.22	1.11	1.22	1.11	1.17	9.02	5.13	4.10
6	1.17	0.97	1.17	0.97	1.19	17.09	18.49	1.68
7	1.10	1.12	1.10	1.12	1.32	1.79	15.15	16.67
8	1.04	0.99	1.04	0.99	1.10	4.81	10.00	5.45
9	1.00	0.79	1.00	0.79	0.95	21.00	16.84	5.00
10	1.08	0.89				17.59		
11	0.99	0.62				37.37		
12	0.91	0.67				26.37		
13	1.25	0.87				30.40		
14	1.20	0.78				35.00		
15	1.89	1.36				28.04		
16	1.37	1.20				12.41		
17	1.03	1.18				12.71		
18	1.02	1.08				5.56		
Average	1.16	0.97	1.12	1.12	0.98	19.18	12.4	5.42
Minimum	0.91	0.62	0.93	0.89	0.79			
Maximum	1.89	1.36	1.31	1.32	1.12			
Variance	0.05	0.04	0.01	0.02	0.01			
Standard Error	0.05	0.01	0.00	0.01	0.00			

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Appendix 1. A description of plant species, moss and litter composition was made at each site at the end of the field season. Four control quadrats (two in each half of the experimental plot) were randomly selected. All plants, moss and litter were collected in half of the original quadrat size (*i.e.*, 0.5 m x 0.5 m, randomly selected). Plants were identified in the field, air-dried and brought back to the laboratory for weighing (± 0.001 g).

SITE 1

Species Composition	g m^{-2}	Proportions	Rank
Sedges (attached dead)	52.11	30.84	1
Dryas integrifolia	37.37	22.12	2
Litter	24.21	14.33	3
Sedges (live)	23.93	14.16	4
Saxifrage oppositifolia	19.36	11.46	5
Moss	6.30	3.73	6
Salix arctica	1.85	1.09	7
Forb[1]	1.28	0.76	8
Poa spp.	0.87	0.51	9
Cruciferae	0.65	0.38	10
Salix reticulata	0.46	0.27	11
Silene acaulis	0.46	0.27	11
Polyganum spp.	0.13	0.08	13
TOTAL	168.98	100.00	

1 = Unknown Forb

SITE 2

Species Composition	g m^{-2}	Proportions	Rank
Dryas integrifolia	73.51	26.01	1
Litter	64.59	22.85	2
Moss	53.48	18.92	3
Sedges (attached dead)	45.81	16.21	4
Sedges (live)	20.76	7.35	5
Salix reticulata	12.77	4.52	6
Saxifrage oppositifolia	6.17	2.18	7
Equisetum variegatum	2.55	0.90	8
Pedicularis flammea	1.41	0.50	9
Forb[2]	0.67	0.24	10
Lichen spp.	0.50	0.18	11
Pedicularis capitata	0.24	0.09	12
Poa spp.	0.15	0.05	13
TOTAL	282.61	100.00	

2 = Unknown Forb

Appendix 1. continued.

SITE 3

Species Composition	g m^{-2}	Proportions	Rank
Moss	507.88	85.01	1
Sedges (attached dead)	52.54	8.79	2
Sedges (live)	24.17	4.05	3
Salix arctica	5.23	0.88	4
Litter	3.77	0.63	5
Equisetum variegatum	2.21	0.37	6
Poa spp.	1.34	0.22	7
Forb[3]	0.12	0.02	8
Polyganum spp.	0.08	0.01	9
Cruciferae	0.06	0.01	9
Lichen spp.	0.03	0.01	9
TOTAL	597.42	100.00	

3 = Unknown Forb

Appendix 2. Characteristics of the three sedge meadows sampled.

SITES	1	2	3
Relief	Middle Slope	Middle Slope	Level
Slope	$10\text{-}15^0$	$1\text{-}5^0$	$0\text{-}1^0$
Aspect	NE	NW	SW
Area	40000 m^2	25000 m^2	3750 m^2